THE BUCHANOSTEID ARTHRODIRES OF AUSTRALIA

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SYNOPSIS

The specimens of *Buchanosteus murrumbidgeensis* collected, with two exceptions, by Harry Toombs in 1955 and 1963 are described in detail, including much of the endocranium and most of the head- and body-armour. This species is separated from the type-species as *Parabuchanosteus* and the family is placed in a new order, the *Migmatocephala*, owing to the presence in the head of dolichothoracid as well as brachythoracid characters.

I. INTRODUCTION

Some twenty years ago five fragmentary specimens of arthrodires from the Murrumbidgee Series casually collected in the Burrinjuck region of New South Wales were sent to the Dept. of Palaeontology of the British Museum (Natural History) and these proved of such interest (White 1952) that a member of the staff was sent out in 1955 to examine the area. One of us (H.A.T.) spent two months, April and May, collecting in the area, and with the generous aid given by Dr. Ida Browne and the staff of the Australian Museum Sydney, made a considerable collection. Unlike the five original specimens which had been almost completely weathered out, the new specimens were almost wholly embedded in the very tough limestone matrix. Most specimens shewed little more than a cross-section of bone, and consequently a long programme of development, largely by the acetic acid process (Toombs 1948), was necessary. However, the results exceeded expectations and in 1963, from May to July, a further visit was paid to the Murrumbidgee area and this was equally successful.

The total number of macro-specimens collected in the two visits was about 500, but of these rather less than one-half were of immediate value. There was in addition a rich assemblage of micro-fossils in the residues and of these the palaeoniscid scales have been described by Schultze (1968) and other material briefly noted by Ørvig (1969*b* : 317).

The material in these collections came from 133 localities, 51 in 1955 and 88 in 1963, with only 6 duplicated. These localities were in two discrete areas some 30 to 40 miles northwest of Canberra. Most of the specimens were found on or near the banks of the Murrumbidgee River, from a little above the new Taemas Bridge downstream to the Burrinjuck Dam, a distance of some 7 to 8 miles. A few however, came from near Wee Jasper, on the Goodradigbee River, a tributary which joins the Murrumbidgee just above the Burrinjuck Dam.

Most of the collecting was done in the Spirifer yassensis Limestone (see Text-fig. 25), but a few specimens were found to range as far up as the Crinoidal Limestone near the top of the Murrumbidgee Series, so that virtually the whole of that series is represented.

These marine beds were at one time considered to have been of lower Middle Devonian age, but more recent work on conodonts and various invertebrate groups has shewn them to be referable to the upper Lower Devonian (Siegenian-Emsian: Pedder, Jackson and Philip 1970).*

The great majority of the macrofossils were fragments of arthrodires representing at least seven genera and species, all of great interest.

Nearly all the material consists of isolated and usually broken plates and bones, and apart from head-material, in only two instances are two or more bones associated. However, in one species part of the endocranium has been preserved and it is with that species that the present paper is chiefly concerned.

This fish was originally described as a new species of the genus *Buchanosteus*, *B. murrumbidgeensis* (White 1952 : 267) on the assumption that it was congeneric with Hills' (1936) *Coccosteus osseus* which Stensiö (1945 : 8, 24) later made the type of a new genus of dolichothoracids, *Buchanosteus.* However, certain features described below seem so very distinct that we have ventured to separate this species as *Parabuchanosteus*, which with *Buchanosteus* forms the family Buchanosteidae (White 1952 : 266). Owing to the imperfection of the material of both species originally referred to *Buchanosteus*, the family was placed in the brachythoracids and the head of *B. murrumbidgeensis*, based on a narrow diagonal slice, was restored on that premise. However, the new material shows that the front of the head, with an independent rostro-pineal bone, clearly favours the dolichothoracids. Stensiö (1963 : 66 footnote, also 7, 95–110, 118, 120–123, 390) has already suggested that the *Buchanosteus* in its mixture of characters might represent a new Order intermediate between the Dolichothoraci and Brachythoraci and tentatively adds *Gemuendenaspis* (Miles 1962) to the group. The last named, like the two other supposed 'mixed' arthrodires from the Northern Hemisphere, *Euleptaspis* and *Tityosteus*, is now accepted as a true brachythoracid (Miles 1969 : 153), but the buchanosteids are placed in a separate Order, the Migmatocephala, by reason of the definiteness of the two groups of characters.

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*Thomson & Campbell (1971 : 18) now propose to put the top beds, the Warroo and Crinoidal Limestones, back into the Eifelian—see Text-fig. 25.

II. SYSTEMATIC DESCRIPTION

DIVISION EUARTHRODIRA

Order MIGMATOCEPHALA nov.

(Gr., μιγμα,το, mixture; κεφαλή, head)

Euarthrodires shewing both well developed dolichothoracid and brachythoracid characters. Anterior part of skull-roof with separate rostro-pineal bone and broad, short preorbital plates with complete mesial contact; orbits large and directed obliquely forwards. Pattern of remainder of plates of skull-roof, of the sensory system and of the known body-plates typically brachythoracid.

At first glance the endocranium seems dolichothoracid in character, but so little is known of the brachythoracid endocranium and that only of specialized forms, that the endocranium of *Parabuchanosteus* may very well be the generalized form for both groups (see p. 406 *infra*).

Family **BUCHANOSTEIDAE** White, 1952

Diagnosis. As for Order (sole family).

Genera. *Buchanosteus* Stensiö (1945 : 8, 24) and *Parabuchanosteus* gen. nov.

Genus ***PARABUCHANOSTEUS*** nov.

Diagnosis. A buchanosteid arthrodire with spade-shaped parasphenoid, as wide as long, bearing numerous fine denticles, largest medially in front and crossed towards rear with a deep groove not quite reaching sides of plate and pierced by a pair of foramina in centre.

This diagnosis is of necessity brief and very incomplete since there is relatively little to compare it with in the unique type specimen of *Buchanosteus*(Hills 1936). The other obvious points of difference such as the concave posterior margin of the head-shield, the fine tubercular ornament and the apparent differences in the development of the central sensory canal and the posterior pit-line are likely to be at the most of specific rank; but the form of the parasphenoid, of its transverse groove and dentition are indication of more fundamental differences which cannot be established until further material is found in the type Buchan area (see Summary of Characters, p. 27).

Type species. The only species, *Buchanosteus murrumbidgeensis* White, 1952 : 267.

Parabuchanosteus murrumbidgeensis (White)

(Text-figs 1–24; Pls 1–9)

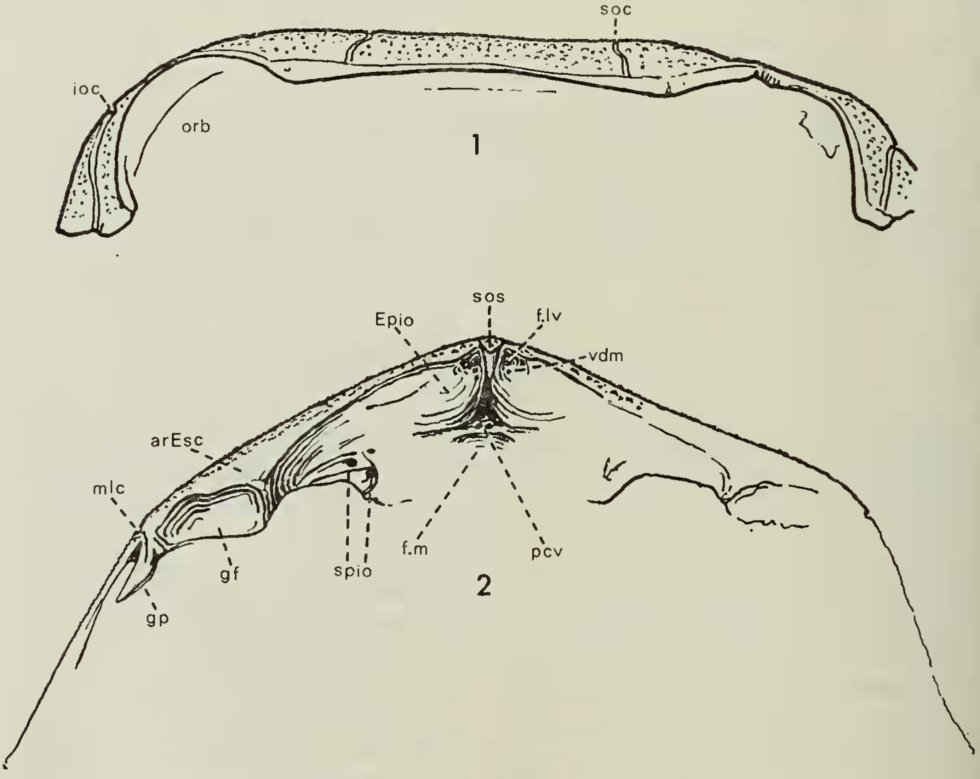
1952. *Buchanosteus murrumbidgeensis* White: 267, Text-figs 20–27; pl. 30; pl. 31, figs 1, 2.

DIAGNOSIS. As for genus (sole species).

MATERIAL. The new material comprises 43 registered specimens of which 31 belong to the head-region, the remainder to the body. The head material includes 3 almost complete head-shields, one with much of the endocranium attached, and two half-heads also with the parts of the endocranium preserved. All the plates of head and body are relatively fragile.

FORMATION AND LOCALITIES. Age. Siegenian-Emsian (see foot-note p. 380). All but 11 specimens come from the Spirifer (Spinella) yassensis Limestone (see Text-fig. 25).

Those from the later beds range from the Bloomfield Limestone possibly to the Crinoidal Limestone, the most satisfactory being the left postorbital-marginal region



Parabuchanosteus murrumbidgeensis (White)

FIG. 1. Skull-roof, front view. P.48672 $\times 1\frac{1}{3}$.

FIG. 2. Skull-roof, back view. P.48672, with additions from P.33597, P.33683A, P.33642, P.48676. $\times 1\frac{1}{3}$.

of a skull-roof (P. 50367) from near the base of the Warroo Limestone at locality 1963/12. The only specimen that might have come from an older stratum is a large fragment of the skull-roof (P. 33430) collected by Mr. D. J. Cameron from the "Lower Limestone" to the NE of the Old Taemas Bridge, and its location suggests that it came from the Cavan Bluff Limestone: if so, the geological range covers most of the Murrumbidgee Series.

These 43 specimens were collected at 26 different localities scattered throughout the collecting area (see p. 411 for list).

DESCRIPTION OF SPECIMENS. THE SKULL. The skull-roof of *Parabuchanosteus* has several remarkable features. The three reasonably complete specimens, are P. 33592, P. 48672 and P. 48675, but several others add worth-while details, especially P.48676, P.33597 and P.48674 and the fragments P.33510, P.33642, P.33635, P.33683*A*.

As shewn by Stensiö in *Buchanosteus* (1963; 115, 121, 122; 1971 : 59), *Parabuchanosteus* had paired rhino-capsular bones enclosed in a discrete rostral exoskeletal capsule.

The component plates of the skull-roof are so intimately fused together that their outlines are generally obscured and no one specimen shows them all—indeed, in the third skull P.48675 (Pl. 2, fig. 3; Pl. 4), to which much of the endocranium is attached, no sutures at all can be traced. The only completely free roofing-plates are a left postorbital (P.50252) and a paranuchal (Plate 7, figs. 1, 3), and it is only a few fragments of plates from large specimens, such as two marginals (P.50382, P.50507) and a paranuchal (P.33202), that shew parts of overlapped areas, indicating that contrary to usual conditions found in vertebrates, the plates of presumably older specimens tend to be freer than in the young.

The most complete skull-roof, P.48672 (Pl. 1, fig. 1) measures in midline 97 mm from the back of the nuchal (*NU*) to the front of the pre-orbitals (*PrO*) and has a maximum breadth of 144 mm, measured over the curve at the level of the postmarginals (*PM*). This skull-roof, like the less perfect P.48675 (Pl. 2, fig. 3) is apparently very little distorted and over all is strongly convex. In front, the central area is slightly concave (Text-fig. 1) passing into a large rounded angle over the orbits so that the post-orbitals (*PtO*) are only 20°–30° from the vertical. In the posterior half (Text-fig. 2) the central part is gently convex and passes on each side into a straight or slightly concave upper plane still formed by the nuchal, and this in turn at about the nuchal-paranuchal boundary, passes into a lower, also slightly concave, plane at about 40° to the other.

The largest of the three most complete skull-roofs, P. 33592, which is much flattened and sliced across by natural micro-faults, is 108 mm in length and a little over 160 mm in maximum breadth; while the third, the most imperfect of the three skull-roofs, P.48675 (Pl. 2, fig. 3), measures approximately 100 mm along the midline and 162 mm (left side ×2) over the curve.

The most intriguing feature of the skull of this arthrodire is that in the pattern of the roofing-bones as far forwards as the front of the centrals (*C*, Text-fig. 3), in the very well developed articular mechanism on the paranuchals and anterior dorso-lateral plates (*ADL* Pl. 7), and in the general distribution of the sensory canal system apart from the primitive position of the occipital cross-commissure on the nuchal plate, the roof is coccosteid, as Hills (1936) clearly indicated. But in front of the centrals in the wide, very short pre-orbitals, the separate rostro-pineal bone, and in much of the form of the endocranium the skull is dolichothoracid in character.

At the back of the skull on the paranuchal plate there is a smooth triangular bevelled area reaching from near the supraoccipital spine to the outer margin of the glenoid fossa, for overriding by the extracapsular plate (*arEsc*, Text-figs 2, 3; Pl.7), which must have nearly, if not completely, filled the nuchal gap between head-shield and body-armour since there is a corresponding area on the anterior dorsolateral plate.

A similar smooth articular area for the anterior lateral plate is shared by the paranuchal and postmarginal plates (*arAL*. Text-fig. 3, Pl. 7), but not in all specimens, for in at least three specimens (Pl. 1, fig. 2; P. 33642, P.50408) this area is as strongly tuberculated as the rest of the shield.

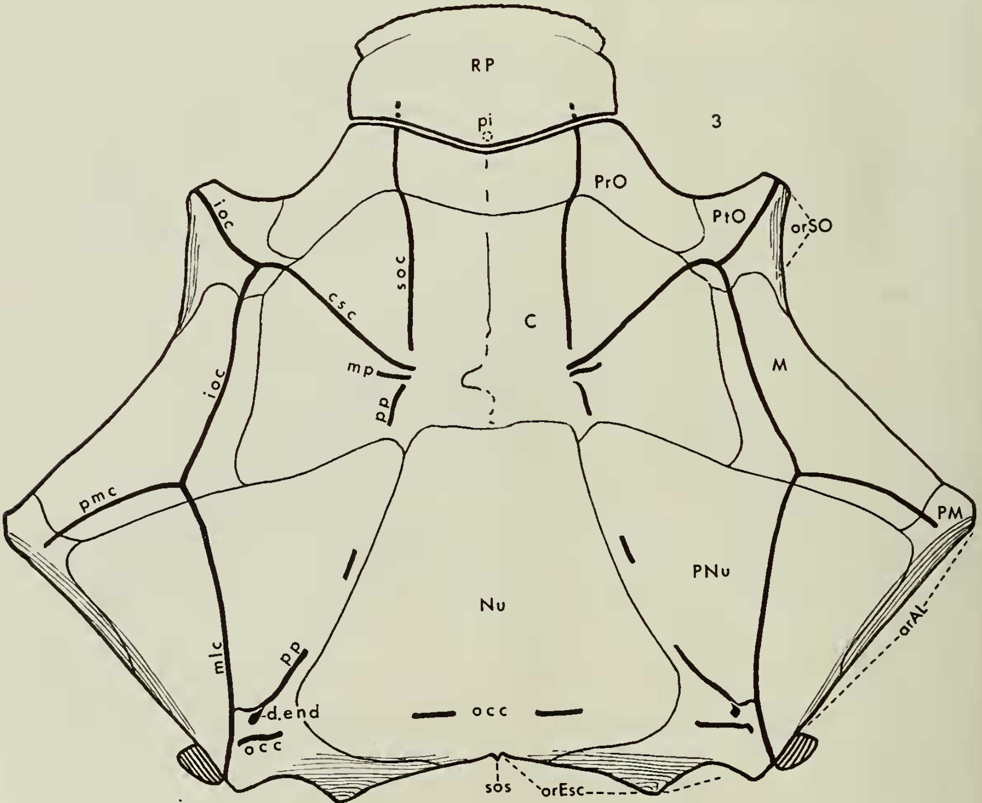


FIG. 3. *Parabuchanosteus murrumbidgeensis* (White)
Restoration of skull-roof, flattened. ×1. See Pl. 1, fig. 2.

Yet a third but small smooth area is present chiefly on the postorbital plate for the overriding of the suborbital (*arSO*, Text-fig. 3).

THE ENDOCRANIUM. The dorsal surface of the endocranium is completely fused to the skull-roof (Pl. 1, fig. 1). In only two specimens are substantial parts of the underside of the endocranium preserved: P.48675 (Pl. 2, figs 1, 2; Pl. 3, fig. 2; Pl. 4) shews it from the forepart of the parasphenoid (*Psph*) for about half the length of the skull and also most of the left side; while in P.33597 (Pl. 5, fig. 2) there is still much of the left and central posterior region in place. From these two one can deduce the general form, very low and wide with the oral surface gently concave across the roof of the mouth and also lengthwise, especially in the sub-pituitary area.

The parasphenoid is preserved in three of the specimens: P. 48672, P. 48675, P.48676, the plates showing a slight increase in size and, possibly, age in that order but also a very marked increase in decay or resorption.

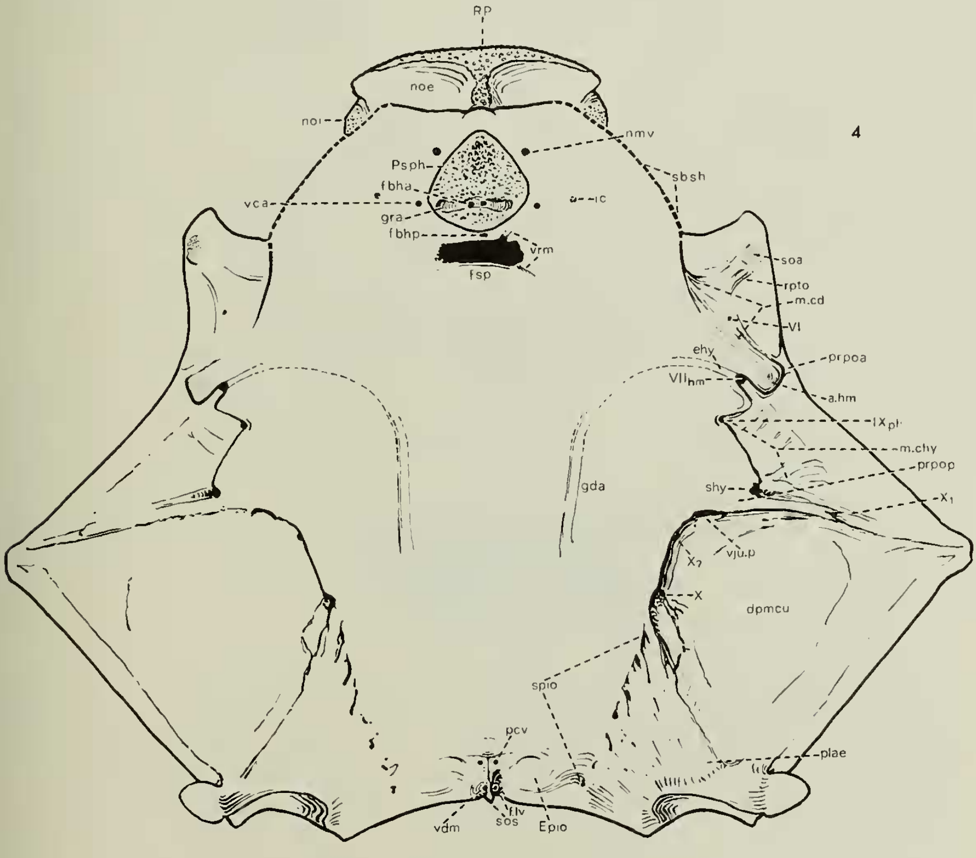


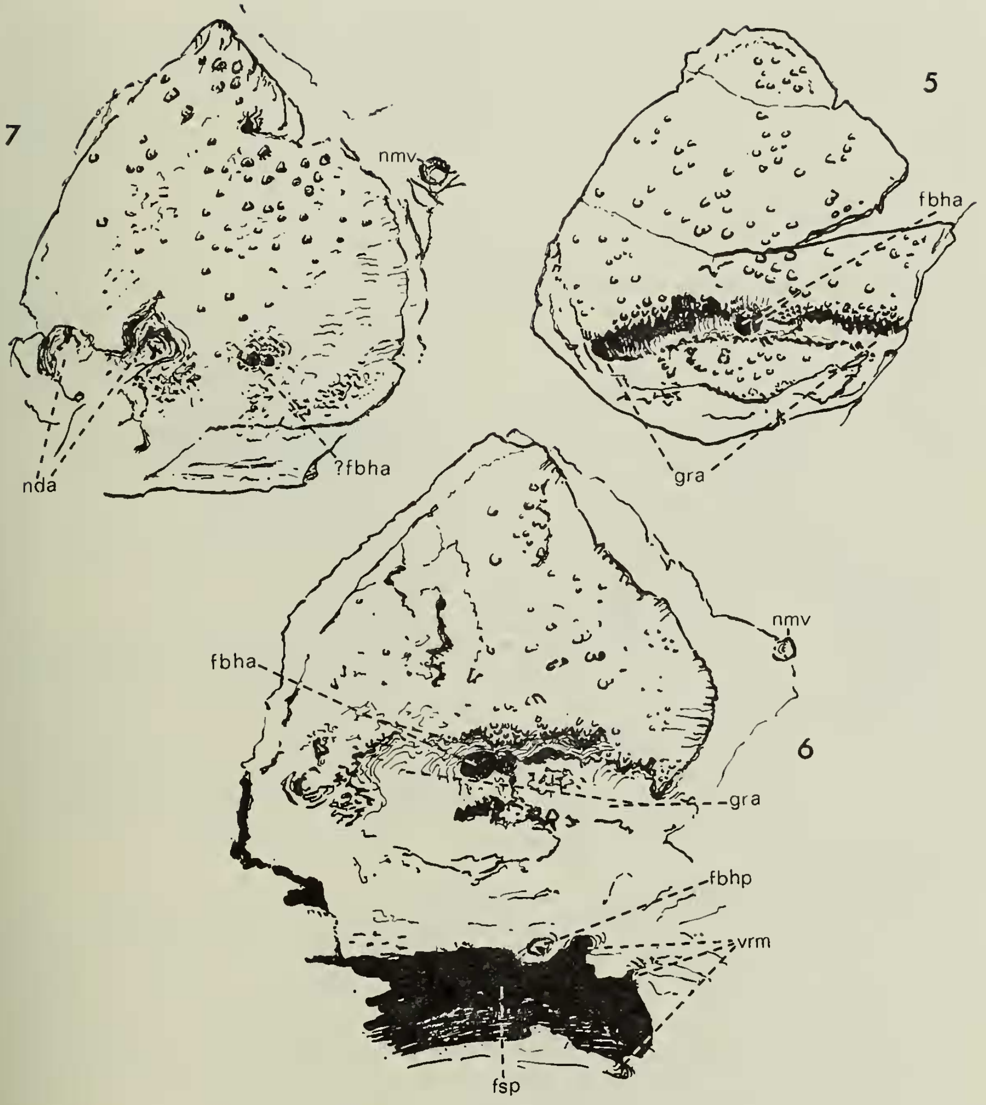
FIG. 4. *Parabuchanosteus murrumbidgeensis* (White)
Restoration of undersurface of skull, flattened. ×1. See Pl. 4.

These parasphenoids are broadly spade-shaped (Pl. 3; Text-figs 5–7), about as long as wide, measuring approximately each way 14·5 mm, 16·4 mm and 18·0 mm respectively, and so differ in shape considerably from the plate described and figured by Hills (1936: 221–2, text-figs, 4, 5) and later by Kulczycki (1956 : 106–7, pl. 1, fig. B) and Stensiö (1963 : 97–100, 121–2, text-figs 37, 44). The surface of the first and best preserved specimen (Text-fig 5; Pl. 3, fig. 1) is nearly flat and almost completely covered by numerous conical denticles, largest at the centre towards the front, and mostly with somewhat worn, rounded tips especially in the front where they were well-placed for grasping. The structure of the spongy middle layer shews through the very thin laminar outer layer between the teeth. The most marked feature of the plate is the very conspicuous groove (*gra*) which runs across the plate almost, but not quite, to each margin, deepening as it goes and slightly bowed forwards. In the centre of the groove where it is shallowest are small twin openings such as Hills identified as 'hypophysial fenestrae' and Stensiö as paired buccohypophysial foramina, (*fbha*), the right (left of figure) substantially larger than the left. But other features described by Hills are hard to reconcile with what is to be seen in our specimens. He writes of a large foramen on each side of the 'fenestrae hypophyseos'—these openings are relatively much larger in his than in our specimens—'which leads upwards into a blind sac-like pit running laterally within the bone. A smooth tract of bone surface runs between these foramina posteriorly to the fenestrae hypophyseos, and it is clear that some strand of tissue or vessel ran from one foramen to the other beneath this smooth tract'. Further he notes that 'on the nearly vertical edge of this median thickened edge' there is on each side a small ovoid foramen leading into a transverse canal which seems 'to enter the foramen leading to the sac-like pit' and 'may therefore have transmitted those parts of the internal carotid arteries external to the cavum cerebrale . . .'

The blind sac-like pits within the bone and the smooth tract connecting them presumably correspond to the large transverse groove in our first specimen, but there is no sign in any specimen of 'transverse canals' leading into it nor of the minute 'carotid foramina' in front of the 'hypophysial fenestrae'. There is no pit at the ends, but a deepening close to the margin of the plate. In the complete right side (left of fig. 1) this groove stops short of the edge, and probably on the left also. The twin foramina are not in front of the groove as in Hills' fossil but actually in it, as in *Dinichthys* cf. *pustulosus* of Kulczycki (1956, pl. 1, fig. G). Moreover, the sides of the groove bear denticles but the floor is smooth.

Dorsally the parasphenoid is expanded over its hinder part, that is the area overlying the transverse groove, into a thick-walled, dome-like outgrowth in which the ventral division of the hypophysis occupies, in young specimens at least, an unspecified part. This expansion, best seen in the following specimen, then passes into a narrow neck through which the lumen grades into the hypophysial fossa, here seen as a deep, otherwise featureless depression about twice as broad as long.

In the slightly larger, and presumably older specimen (P.48675, Text-fig. 6; Pl. 3, fig. 2) the transverse groove has been greatly widened by resorption or decay of the bone and this has left a very rough surface indeed of the cancellar layer, but the dentition, much worn in front has persisted and, although overall generally thin, is



Parabuchanosteus murrumbidgeensis (White)

FIG. 5. Rather small relatively unworn parasphenoid shewing crowded teeth and well preserved transverse groove for the 'Rachendachhypophyse' (*gra*) and twin anterior buccohypophysial foramina (*fbha*). P.48672 ×4. See Pl. 3, fig. 1.

FIG. 6. Part of roof of mouth shewing parasphenoid and subpituitary fenestra, the former with the transverse groove for the 'Rachendachhypophyse' and the surface posterior to it partly resorped. P.48675 ×4. See Pl. 3, fig. 2.

FIG. 7. Imperfect parasphenoid with oral surface completely resorped but with sparse pointed teeth re-grown in anterior region. P.48676 ×4. See Pl. 3, fig. 3.

thickly clustered along the anterior lip of the groove. In spite of this resorption the groove has been extended to break through the plate only on the left side (right of figure), but on the other side a shallow depression has been developed independently to the side of the groove. The whole surface is extremely rough and the apertures of the paired bucco-hypophysial canals (*fbha*) are much enlarged and confluent, passing immediately into a chamber above, the ventral part of the fossa hypophyseos.

A fragment of the canal of the left naso-maxillary vein (*nmv*) lies well outside the parasphenoid.

In the third specimen (P.48676, Text-fig. 7: Pl. 3, fig. 3) the parasphenoid and neighbouring vessels have been twisted out of the mid-line. Almost the whole surface of the plate has been resorped and all trace of the groove save for one or two faint depressions has disappeared. The right side (left of figures) shews a deep irregular pit which may be due either to decay or to post-mortem effects and on the left side, some distance from the centre is a pit in which is a circular perforation, and this too is unlikely to have any connexion with the living design.

The teeth are much sparser than even in the last specimen. The large very worn teeth have persisted in front, but here and there elsewhere small sharp teeth give the impression of being regenerated rather than residual, especially as one occurs within the 'crater' of the perforation mentioned above.

The persistence of the anterior part of this plate in both second and third specimens at the time the rest of the plate has undergone profound alteration is most puzzling, particularly in relation to the transverse groove, which in any case seems unlikely in its form and impersistence, let alone its nearness to the surface of a biting plate, to have housed a blood vessel, especially such an important one as Stensiö's (1963 : 122, text-fig. 44) 'Sub-hypophysial transverse anastomosis of the internal carotid arteries'. If such an anastomosis were present, one would expect it to pass above the parasphenoid, as in *Tapinosteus* and *Pholidosteus* (Stensiö 1963 : 211, text-figs. 63, *gr.a.com.;* 68*B*, 69*B*, *a,com.*).

These objections apply with still greater force to Kulczycki's suggestion that the small central foramina are those of the internal carotids themselves (1956 : 107–9, pl. 1, *c.aci*). Another suggestion that has been put forward is that the true homologue of the transverse groove, whether complete or divided (*cf.* Miles & Westoll 1968 text-fig. 18*a*, *gr.a.com*) is the 'prespiracular groove' of *Glyptolepis* (Jarvik 1954 : 39, text-fig. 20, *gr.psp*). However, Kulczycki has already repudiated this idea on account of the supposed lack of denticles in the groove in arthrodires and the presence of the 'bone-bridge'. Indeed, the smooth broad shape etc. of the under face of the endocranium bears little resemblance to that in the crossopterygian.

Attention may be more profitably directed to the hypophysis in chimaeroids, in which there is a marked extra-cranial (oral) component, the 'Rachendachhypophyse'. In small specimens of *Hydrolagus* it is "in the form of symmetrical tubular structure in cross-section' but in the adult it is 'three times as large as that of immature animals' and 'a massive compact organ' (Sathyanesan 1965: 414–7, figs 1–12).

Meurling (1967 : 89, 102) in his study of *Chimaera* discusses the possible homologies of the Rachendachhypophyse, either with the ventral lobe of the pituitary of elasmobranchs, or as an outgrowth or remnant of the hypophysial stalk. The latter is the more relevant to our purpose. The depression in the cranial base which lodges it is, according to Allis (1917 : 115), a remnant of the hypophysial fenestra, so marked a feature in some arthrodires (Stensiö 1963 : 137, figs 14, 15, 36*c*, 47*a* etc), and this is still open in embryos and, importantly, sometimes in young specimens (Fujita 1963).

There are then features which provide grounds for suggesting that the sub-hypophysial transverse grooves in the parasphenoid of *Parabuchanosteus* may have housed an organ comparable to the Rachendachhypophyse in living chimaeroids, such as its position relative to the hypophysis and to skull base and mouth, and its

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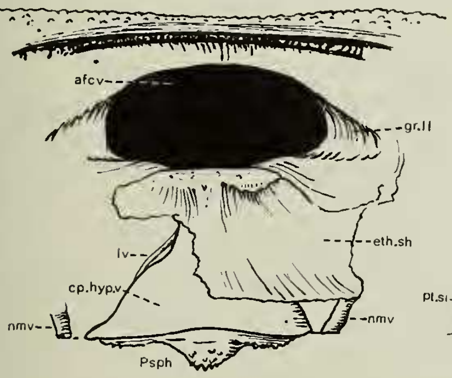

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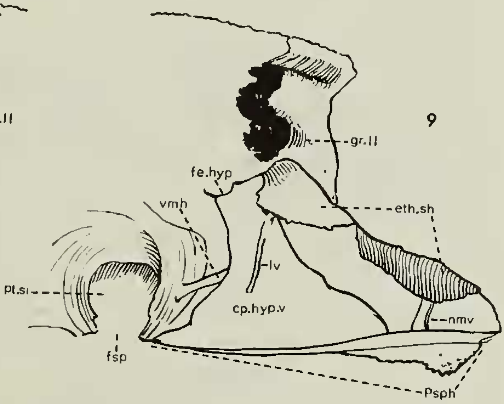

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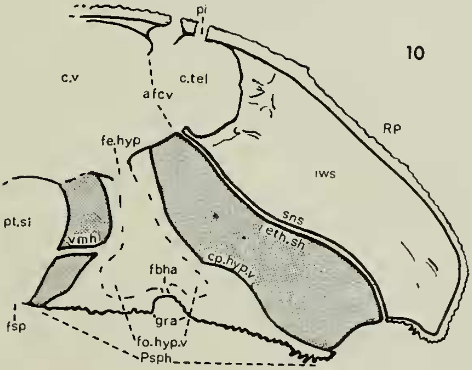

Parabuchanosteus murrumbidgeensis (White)

Fig. 8. Direct front view of imperfect post-ethmoid part of skull, partly restored. Based largely on P.48675. ×2 approx. See Pl. 2, fig. 2.

Fig. 9. Slightly oblique right lateral view of same with part of side wall removed. ×2 approx.

Fig. 10. Diagrammatic median longitudinal section through rostropineal bone and anterior post-ethmoid region. ×2 approx.

twinned form. Its broad transverse form is to some extent paralleled by the 'posterior transverse part of the hypophysis' which Stensiö (1963 : 95 text-fig. 36) postulated as occupying the broadest, posterior part of the bucco-hypophysial foramen 'corresponding to the broad, transverse hindmost part of the embryonic hypophysis of the Selachians'. That such an organ should in older specimens disappear with the general atrophy of the parasphenoid is curious, but we do not yet know fully the function of this part of the hypophysis, and in any case its disappearance is not so remarkable as that of an artery would have been (*cf.* Stensiö 1963 : 97 text-fig. 37D).

In a later brachythoracid, *Tapinosteus* (Stensiö 1963, *c.t.* text-figs. 48, 71, etc.) this transverse groove is reduced to a pair of canals 'terminating in interior of the parasphenoid (without any opening into the fossa hypophyseos)' on either side of the pair of very small buccohypophysial canals.

The other remarkable feature shewn on the broad ventral surface of the endocranium is the large transverse fenestra immediately behind the parasphenoid. This underlies a very large pituitary sinus (*fsp*;*pt.si.*, Text-figs 9–11) precisely in the position in '*C. osseus*' of Stensiö's 'possible subpituitary fossa', 'groove or canal for pituitary vein' and 'canal for pituitary vein and for the rectus externus muscle of the eye' (1963 : 121–2, *f.sbp.*, *gr.v.pit.*, *c.v.pit.*, see also pp. 48, 56–62, 70, text-figs 14, 15, 20*D–F*, 25, 41, 48*B*, 49*C*, etc.). The supposed differences between the two forms may be partly due to crushing in Stensiö's material with the possibility that in *Kujdanowiaspis* and in the other forms restored after it the median part of the pituitary vein was in fact not 'situated underneath the endocranium', but ran through it. This subpituitary fenestra is only preserved in the one specimen P.48675 (Text figs 4, 6, 9–11, Pl. 2, fig. 1; Pl. 3, fig. 2) and in that only the left side (right of figures) is complete, and this shews that at least two vessels (*vrm.*) entered at the margin of the fenestra, which from the tributary markings on the bone were veins draining from the roof of the mouth into the pituitary sinus.

On each side of the parasphenoid near the anterior end is a conspicuous, nearly vertical canal (*nmv*, Text-figs 4, 6–9, see also Pl. 2, fig. 2, Pl. 3, figs 2, 3; Pl. 4) running up from the roof of the mouth, which was possibly for the naso-maxillary vein, while further behind is the foramen of the anterior cerebral vein (*vca.*). Little further out from this must have been the internal carotids, but the area is not preserved.

The only other feature shewn on the remnant preserved of the general surface of the endocranium is the faint impression of part of the left dorsal aorta (*gda*).

The left (right of figures) marginal area is largely intact in P. 48675 (Text-fig. 4; Pl. 4) behind the level of the post-orbital (*PtO*), but the suborbital shelf and, if any, the ectethmoid process are missing in all specimens.

The first feature of interest is the ridge under the postorbital plate (*rpto*) at the distal end of which is the articular head for the suborbital plate (*soa*). This ridge is the 'anterior postorbital process' in Stensiö's (1963 : 120, text-fig. 44, *pr.poa*) restoration of *Buchanosteus* and between this and the true anterior postorbital process (*prpoa*) is the area for the dorsal attachment of the *m. constrictor dorsalis* (levator palatoquadrati; *m.cd* Text-fig. 4, see Edgeworth 1935 : 46, figs. 110, 111, etc.) and a foramen possibly for the abducens nerve (VI). The end of the process is always unossified and presumably bore a cartilaginous area for the articulation of the hyomandibula (*a.hm*). Immediately behind is a deep invagination leading to the canal for the hyomandibular branch of the facialis nerve (*VIIhm*), and below this the groove for the efferent hyoid artery (*ehy*). A smaller invagination shortly behind is possibly for the exit of the pharyngeal branch of the glossopharangeal nerve (*IXph*). Between this and the posterior postorbital process (*prpop*) the floor of the endocranium projects, so that the side is concave and is marked by a series of parallel ridges which are continued on to the underside of the skull-roof (*m.chy*) being the attachment scars of the upper side of the *m. constrictor hyoideus* (Edgeworth 1935 : 98, fig. 110, etc) and possibly also for the *m. adductor mandibulae.* Other details of this region may be seen in the much fractured right side (Text-fig. 11; Pl. 2, fig. 1) which gives a lateral view of parts of some of the canals inside the endocranium (*cf.* Stensiö 1963, text-fig. 28). Conspicuous in front is the exit of the efferent pseudobranchial artery (*psba*) which passes into a large anterior myodome, and shortly behind that is the exit of the oculomotor nerve (III) with possibly a second myodome for the superior oblique eye-muscle. Immediately below is the relatively enormous pituitary sinus (*pt.si*) above the sub-pituitary fenestra (*fsp;* see also Pl. 2, fig. 2 and Text-figs. 6, 9, 10), leading into a very large posterior myodomal space (*pt.my*), for the rectus eye-muscles. This is as in Stensiö's description ot *Kujdanowiaspis* (1963 ; 55–56, 58, text-figs 14, 17, 30, 41 *et al.*) except that there the pituitary vein and the posterior part ot the *m. externus posterior* are 'extra-mural', and lie in a sub-pituitary fossa, and this fossa is also shewn in an undetermined dolichothoracid from the Lower Devonian of Spitsbergen, while *Buchanosteus* has been similarly endowed in restorations (Stensiö 1963, *f.sbp* Text-figs 15,44).

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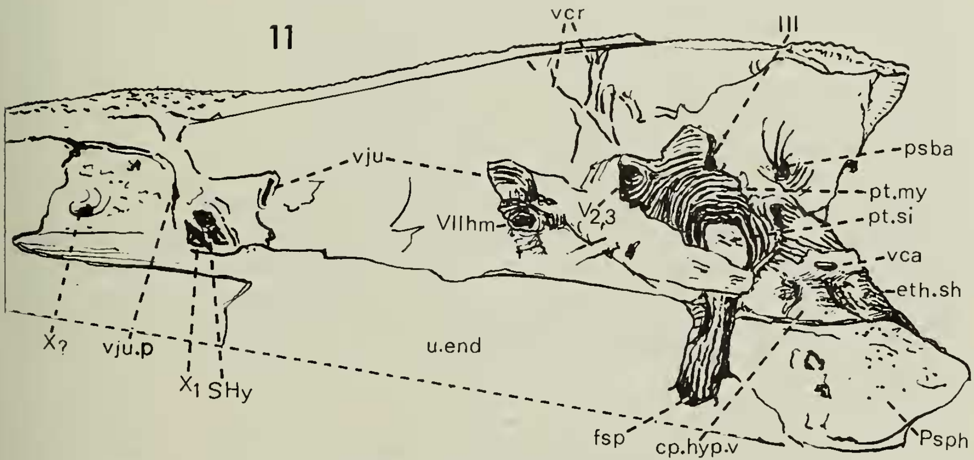

FIG. 11. *Parabuchanosteus murrumbidgeensis* (White).
Right anterior half of fragmentary endocranium somewhat tilted upwards. P.48675 ×2.
See Pl. 2, fig. 1.

That author has given a possible explanation of the 'extra-mural' position of the pituitary vein on embryological grounds, but it seems nevertheless remarkable to find this important difference in two genera, *Kujdanowiaspis* and *Parabuchanosteus* which have otherwise many features in common in this part. If the rectus externus muscles do come so far in, one may wonder why they would need such a powerful attachment.

Above the sinus on a level with the efferent pseudobranchial canal is a small foramen possibly for the oculomotor nerve (*III*) and further still to the rear at a somewhat lower level in the illustrations the broken exit of the 'trigeminus proper' ($V_{2,3}$), which corresponds reasonably well with Stensiö's interpretation of the details in *Kujdanowiaspis* (1963, text-fig. 17). Above $V_{2,3}$ are a number of small canals leading into the skull-roof possibly for nutritive vessels (*vcr*) (*cf.* Ørvig 1957 : 307, text-fig. 6) leading to the sub-cutaneous vascular plexus (see p. 393 *infra*). A little behind these near the floor of the endocranium is a section of the canal of the hyomandibular nerve (*VIIhm*) marking the position of the anterior postorbital process on this side, and attached to the canals upper surface as in dolichothoracids and coccosteomorphs (Stensiö 1963 : 282), is an anterior fragment of the jugular canal (*vju*) leading into the posterior myodomal space. A hinder fragment of this canal is to be seen similarly placed to the two canals (IX, X_1) extending from the posterior postorbital process, which is complete on the other (left) side (Text-fig. 4; Pl. 4, also Pl. 5, fig. 2).

The posterior postorbital process is an interesting development. When Stensiö (1945 : 12–13, 32, text-figs. 5–7) first dealt with this part in *Kujdanowiaspis*, in which it is forked, he described the posterior branch as being hollow and carrying the *v. posthyoidea lateralis* to the jugular vein. Later (1963 : 70, 82–84, text-figs 14, 41, 42*C*, 43, etc.) the two shanks are shewn to be solid and appressed to the underside of the paranuchal and postmarginal plates, and it was suggested that these shanks of the posterior process 'may very well have been formed from the posterior parts of two long, dorsal extra branchials originally belonging to the hyoid arch and to the branchial arch proper (the glossopharyngeus arch), respectively.'

The posterior postorbital process in *Parabuchanosteus* is very different and it is difficult to reconcile its form with the origin suggested above.

The jugular vein between the anterior and posterior postorbital processes runs entirely inside the endocranium in *Parabuchanosteus**, which it leaves by a large aperture at the base of the hinder face of the posterior process (*vju.p*). The latter is broad at the base and very long, and when undamaged reaches almost to the outer edge of the post-marginal plate. It lies directly under the post-marginal sensory canal and is therefore attached to the under-surface of the marginal for the greater part of its length and does not underlie the paranuchal plate at all, as it does in *Kujdanowiaspis*. It consists of a narrow tube for most of its length, as well preserved specimens show (P.33635, P. 33642), and then continues as a groove to the postero-lateral angle of the shield. At the proximal end immediately inside the

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* There seems to have been the same arrangement in *Stuertzaspis* (Westoll & Miles 1963 : 150, text-fig. 4), the supposed perforation of the anterior post-orbital process (*c.v.ju.m*) being the foramen of *VII hm.*

endocranium it passes over the jugular vein just before the latter leaves the skull at *vju.p* (P.48675). This canal carries the first branchial trunk of the vagus nerve (X_1) and not the hyoid vein, as I first described it (White 1952; 272–4, text-figs 22–25). The process is completed by a well marked groove and ridge running along its anterior side for about one-third of its length. The groove continues a large canal which passes into that of the jugular vein; and which is now identified as that for the hyoid vein, although such a position, as Holmgren (1942 : 170) has remarked, is much further forward than is the case in sharks (*sh.y*, Text-figs, 4, 11; Pl. 2, fig. 1. *cf.* Westoll & Miles 1963 : 144, 150; Miles & Westoll 1968 : 403).

Nothing of any value has been found in the labyrinth area, but fragments are to be seen in P.48672 (*r.la.c.*, Pl. 1, fig. 1.) and in P. 33597.

The posterior postorbital process marks the anterior boundary of the large cucullaris depression (*dpmcu*), and inwards and backwards of the posterior opening of the jugular vein canal (*vju.p*) to the main exit of the vagus (*X*) the side of the endocranium is dorsoventrally concave for the attachment of muscle. Along this reach is a foramen (*X*?), perhaps for the second branchial trunk of the vagus, or for a vein. Behind the main vagus exit (*X*) the endocranium rapidly widens and shallows and ends in a more or less vertical wall, at least in the upper part, along the line of the posterior margin of the skull-roof between the articular processes. There is no discrete supravagal process but this is clearly represented by the postero-lateral corner or angle of the endocranium (*plae*, Text-fig. 2; Pl. 1, fig. 1; Pl. 4; Pl. 5, fig. 2; Pl. 7, fig. 3), and as will be seen later shows that the cranio-spinal process of Stensiö in coccosteids is a true supravagal process and nothing to do with the cranio-spinal process in petalichthyids.

The thickening of the skull-roof pierced by the canal for the endoskeletal division of the endolymphatical duct (*th.n*, *d.end.i*, Plate 4) is much as in *Kujdanowiaspis* (Stensiö 1963, text-fig. 42*C*).

Behind *X* and following the line of the narrowing endocranial wall are the apertures of the spino-occipital nerves (*spio*, Text-figs 2, 4; Pl. 5, fig. 2; Pl. 6, fig. 8). There appear to be at least 7. The anterior nerves appear to have only one large elongated aperture but the fourth and subsequent canals are double, having a smaller upper aperture for the dorsal branches. A few of these canals are very well seen in Pl. 5, fig. 2, coming from the cranial cavity, the only instance in this material when a substantial part of the cavity wall has been preserved, except part of the roof seen in P.48674 (*rcr*, Pl. 5, fig. 1), and the smooth median dorsal tract that runs the length of the underside of the fine skull, P. 48672 (*rcv*, Pl. 1, fig. 1). On either side of the tract in this as in other specimens (*e.g.* P.33592, P.33610, P.58443 etc., but especially P.33642) are vestiges of the subcutaneous vascular plexus already noted above (p. 392) and which have been described and figured in a specimen possibly of *Actinolepis* by Ørvig (1957 : 307, text-fig. 6).

The back of the skull (Text-fig. 2; Pl. 6, fig. 8) bears little resemblance to the types described by Stensiö (1969 : 223–246, *e.g.* text-figs 12, 21, 35, 124) of which the pholidosteid, that which is said to characterize the coccosteomorphs, is hypothetical.

In *Parabuchanosteus* the upper part of the back of the head is vertical and vested in perichondral bone. It is divided by a deep median groove into two very convex

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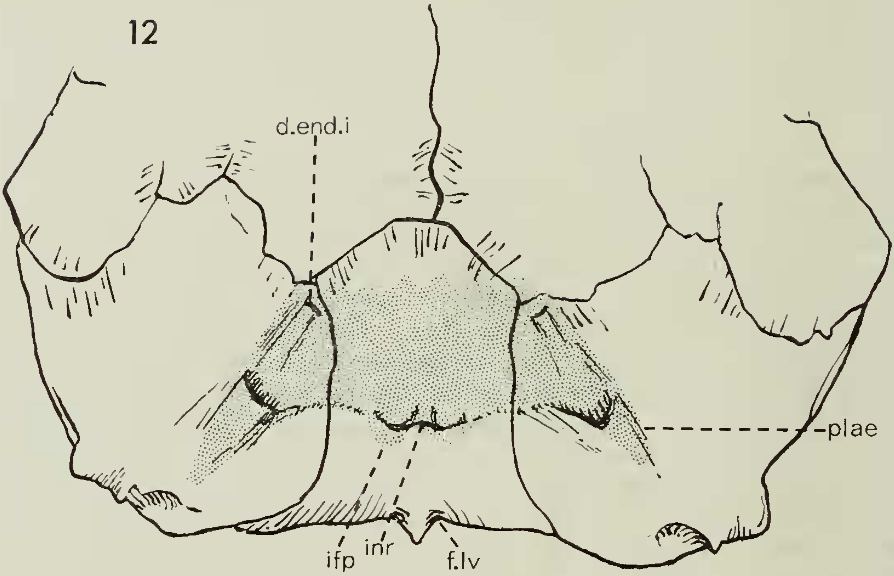

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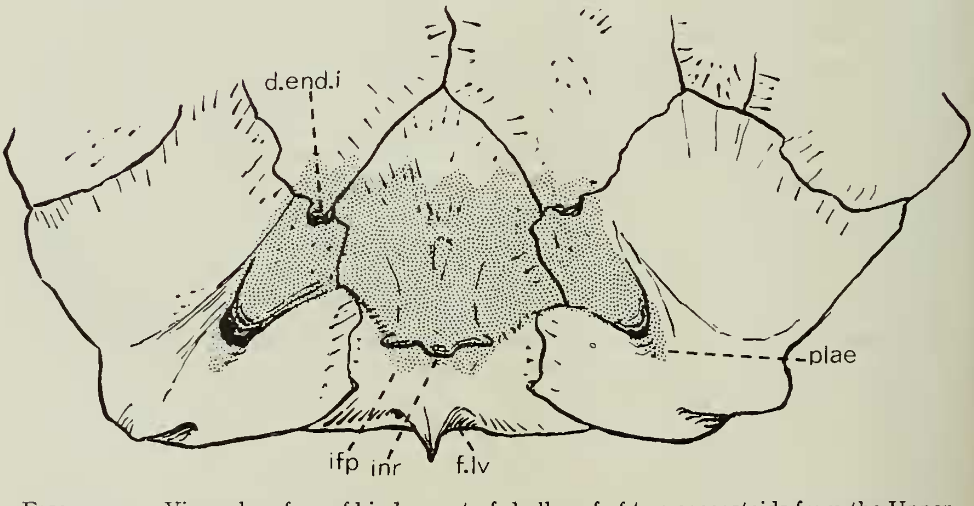


FIGS 12, 13. Visceral surface of hinder part of skull-roof of two coccosteids from the Upper Devonian of Gogo, Western Australia to shew the form of the endocranial roof (stippled). P.50913, P.52551 ×2.

sides, the epiotic prominences (*Epio*), each with a deep pit (*fdv*) flanking the supraoccipital spine (*sos*), which fills the median groove at the top. A pair of well-marked foramina for post-cerebral veins (*pcv*) are at the bottom of the median occipital groove. The spine is attached to part of the skull-roof which appears to be a discrete dermal bone although fused indistinguishably, like the other larger dermal bones, into the skull-roof. In P.33597 (Pl. 5, fig. 2) the occipital surface is broken away and the supraoccipital spine is seen to have the form of an inverted cone. The pits on the occipital surface on each side of the spine have in them a small foramen for a vein (*vdm*), and are the proper areas of attachment for the levator muscles of the head (*f.lv*) and, as already suggested by Miles & Westoll (1969 : 400), not those so designated by Stensiö (1963, *f.lv*, text-figs. 54 *B-D* etc; 1969 text-figs 124, etc.), which are inside the endocranium and are so clearly seen in this specimen. These pits are here named the infranuchal pits (*ifp* Pl. 6, fig. 8*a*) and are separated by the median infra-nuchal ridge (*inr*). They were possibly filled with cartilage to strengthen the very thin endocranial back-wall.

The true arrangement is also shewn quite clearly by the Newcastle specimen of *Coccosteus* figured by Miles & Westoll (1968 pl. 1, fig. B) and Stensiö (1969, text-fig. 124D) and by two skulls of coccosteids from Gogo, Western Australia which Dr. Miles has kindly allowed me to examine and to figure (Text-figs 12, 13). In each case, especially clearly seen in the Australian specimens, the pits face forwards and, as Miles & Westoll have pointed out (1968 : 400, text-figs 2*a*, 16*b*) could not have been for the levator muscles.

In these three specimens only the top of the posterior surface of the skull is preserved in bone (the posterior ascending lamina of Stensiö), and like the remainder of the endocranium, the rest was presumably cartilaginous; but what is present of the back of the skull slopes forwards over the infra-nuchal pits and not backwards as has been suggested in restorations of *Tapinosteus*, *Pholidosteus* and *Coccosteus* (Stensiö 1963, text-figs 46–49, 54 etc.). The true pits for the levator muscles are much smaller and fainter than in *Parabuchanosteus* but distinct nevertheless and in the same position on either side of the supraoccipital spine, which is much larger and completely fused with the back of the skull. There is no vertical median groove, nor are epiotic prominences developed.

The endolymphatic duct runs in a thickening within the endocranium as in *Parabuchanosteus* and *Kujdanowiaspis*, but the thickening is more centrally directed owing to the form of the endocranium.

It is not very difficult to derive this region of the endocranium from that of *Parabuchanosteus* or of *Kujdanowiaspis*.

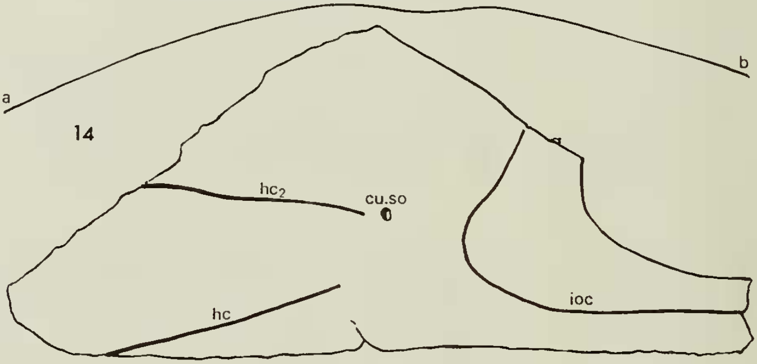
The cervical articular apparatus of *Parabuchanosteus* is very well developed (Text-figs. 2–4; Pl. 6, figs. 5, 7; Pl. 7), the fossa being broad and deep and the processes conspicuous on both the paranuchal and anterior dorso-lateral plates, although varying somewhat in detail. A curious feature of the joint is that in the only complete associated set (Pl. 7) when fitted together there is absolutely no possibility of movement between head and body-armour, even allowing for the articular lining.

ROSTRO-PINEAL BONE. A fairly complete example of the rostro-pineal bone (or rostral exoskeletal capsule of Stensiö 1963 : 115, text-figs. 10*A*, 42, 43) is present

(P.33612, Pl. 6, figs 1–4), and also the left side of this bone from a smaller animal (P. 33629). The former was identified by Dr. Roger Miles who has described it more fully in relation to other material (Miles 1971 : 185, text-figs 104, 105, '*Buchanosteus*'). It is complete on the right side but has lost its roof on the left, and the component bones, pineal, rostral, post-nasal and pre-rostral, if present, are completely fused together.

The triangular subnasal shelf or lamina (*sns*) fits closely on the ethmoid shield immediately below the anterior fenestra of the neuro-cranial cavity (*afcv*, Text-figs. 8–10), on each side of which is a well-marked groove for the optic nerve (*gr.II*).

The posterior face of the postnasal wall is hollowed out to form a deep transverse groove or cavity for the telencephalon (*c.tel*) with the cribrosal area on each side (*fno*, Pl. 6, figs 2, 4) for the passage of the olfactory nerve fila, and above there appears to be the much damaged pineal opening (*pi*). The olfactory tract must have been very short (*cf.* Stensiö 1963, text-fig. 38A). Laterally to the cribrosal



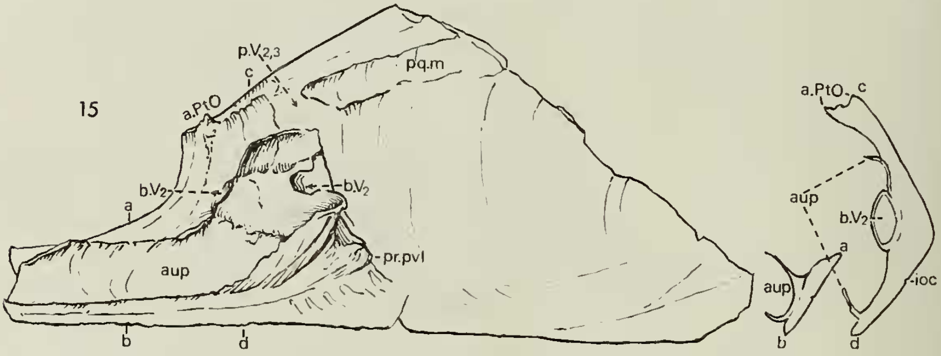


FIG. 14. *Parabuchanosteus murrumbidgeensis* (White).
Outline of right suborbital plate shewing sensory system *ab*, outer longitudinal curvature.
P.50416 × 1½. See Pl. 8, fig. 3.

FIG. 15. Sketch of inner face of same specimen to shew seating of palatoquadrate.
Vertical sections at *ab*, *cd*.

areas the groove of the postnasal wall opens out to form the orbito-ethmoidal 'slit' (*f.nv*) and above the main groove there is a smaller dorsal groove (*dg*) narrow in the centre but wider laterally, through which canals for the profundus (V_1) and the superficial ophthalmic (*oph.V*) nerves passed forwards through the wide internasal wall-space. This groove is continued at the side (*dls*) as far forward as the notch for the inhalent nostril and in it the lateral ophthalmic nerve passed through a short canal or arch (*oph. l*).

The internasal wall (*iw*) forms a large triangular cavity roughly coextensive with the sub-nasal shelf. In it are to be seen the remains of numerous canals for nerves and vessels.

The fenestra exonarhina communis is very large and the nasal cavity each side is divided into a smaller posterior division or depression (*pd.n.cav*) corresponding to the incurrent nostril and a much larger, wider, anterior division (*ad.n.cav*), for the exhalent nostril, and this in front was partly lined with dermal bone bearing denticles in front and medially (*dt*, Pl. 6, figs 1, 3).

There is no interfenestral process separating the nostrils externally and the inhalent nostril, the position of which is clearly indicated by a conspicuous denticulated groove, must have been immediately over the exhalent which was entirely cartilaginous. However, it is not difficult to see how the nasal region of *Kujdanowiaspis* (Stensiö: 1963: text-fig. 10*A*, etc.) could have been derived from such as that of *Parabuchanosteus* by the restriction of the fenestra and its subdivision by the development of the process.

Another bone belonging to the head region that may be referred to this fish with confidence is a right suborbital (Text-figs 14, 15; Pl. 8, fig. 3), which is complete except for the tip of the suborbital bar and the posterior margin. It fits reasonably well on to the middle-sized skull-roof (P. 48672, Pl. 1. fig. 1) although from a somewhat larger specimen, and shews how very forwardly directed the eyes must have been, the orbits being only 40° from direct forward vision. The plate is considerably curved longitudinally and dorso-ventrally. The latter curve is angular with the upper part twice as deep as the lower on the postorbital expansion. The pattern of the sensory system is remarkable. The infraorbital canal runs well behind the orbital continuing after the briefest of intervals the line on the postorbital. Behind it on the upward slope is a pit for a cutaneous sense-organ (*cu.so*) immediately followed by a sensory line gently inclined upwards and below this on the downward slope another line more steeply inclined downwards. This pattern of sensory organs so fully developed is rare in the group (*cf. Holonema:* Miles 1971 : 132, text-figs 32*A*, 33*A*). The lower line may be reasonably identified as the anterior part of the supramaxillary (supraoral) canal (*hc*, Stensiö 1947 : 53, text-figs, 12, 15*B*) while the upper line rather neatly occupies the 'primary position of the probably reduced middle division of the supra maxillary line' (hc_2), *ie.* the post-suborbital line of Miles and Westoll (1968 : 396).

The inner concave face of the suborbital plate is of great interest for the outer margin at least of much of the palatoquadrate was invested with perichondral bone and this is rigidly fused to the inner face of the suborbital plate (*aup, pq.m*, Text-fig. 15). The seating is broad and the outer margin of the autopalatine especially must have been massive. It follows the curve of the orbit and turns upwards giving off as it does a postero-ventral process (*pr.pvl—cf.* Stensiö 1963 : 232, text-figs 51*C*, 70, 77). Almost immediately above this the palatine is pierced by a very large foramen or arch ($b.V_2$), and shortly above this the seating of the autopalatine part is separated from that of the middle part of the palatoquadrate by a wide gap or broken arch ($p.V_{2,3}$). This gap is possibly for the passage of the maxillary and mandibular nerves, of which the former turned forwards and, joined by the lateral buccal nerve, passed through the lower arch ($b.V_2$). The seating of the middle part runs near and roughly parallel with the top of the plate and is only half the width of the autopalatine attachment, and in a fragment from a somewhat larger fish (P.33678) the whole surface is seen to have been covered in bone. The front of this margin at the orbit is broadened with large inner lateral denticles or pegs for attachment to the skull-roof (*a.Pto*, Text-fig. 15).

In general the arrangement of the palatoquadrate in this region bears a very fair resemblance to Stensiö's 'Tentative restoration' in *Kujdanowiaspis* (Stensiö 1963 : 123–5, 199, 206, text-figs 39*A*, *B*, 40).

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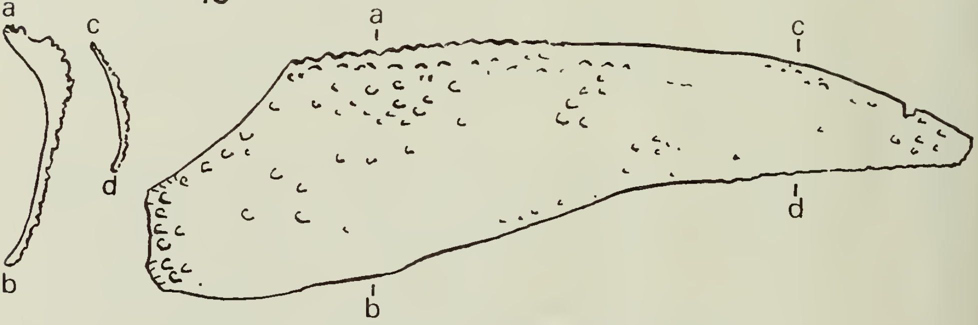


Fig. 16. *Parabuchanosteus murrumbidgeensis* (White).
Right sub-marginal plate with cross-sections at *ab*, *cd*. P.53260 ×3.

The only other part of the head identified in the collections, the submarginal plate, is represented by a single but complete specimen from the right side (Text-fig. 16). It is thin and internally concave, 370 mm long and 10 mm wide at the maximum. Both margins are gently curved, the lower concave except at the back, the upper convex, especially in front, and in spite of the universal tubercular ornament it shews a groove along the marginal contact. At the back it is cut away for the projection of the postmarginal plate.

Body-plates. The body-plates that may be considered in connection with *Parabuchanosteus* are few in number, not more than 13, thin like the head-shields but apparently even more fragile, for all are imperfect, mostly very imperfect, with few margins to establish their shape directly, and generally from smaller animals than the heads.

There is, of course, the difficulty inherent in all assemblages of isolated plates where more than one species is represented (which is here clearly shewn by the presence of two very different types of posterior ventro-lateral plate) of sorting them correctly, particularly in this instance where the ornament is similar in several species.

Fortunately the only associated plates, the imperfect and rather small but finely preserved paranuchal and anterior dorso-lateral plates (Pl.7), provide with their overlapped areas a clear link between the heads and the isolated plates of the back and sides.

There are six examples of the median dorsal plate (*MD*), P.33583, P.33672, P.50346–7, P.50357, P.50389, which although each is imperfect, together give a fair idea of its form (Text-fig. 7; Pl. 8, figs 1, 2).

The shape is simple, perhaps deceptively so, with a straight anterior margin, almost straight sides (there is a slight waist) and an obtuse posterior spine—features that can be found, at least separately, among either coccosteomorphs or pachyosteomorphs (Gross 1932). The plate is fairly elongated, with the maximum breadth over the curve a little less than one-third of the median length, the most complete specimen measuring approximately 48 mm × 155 mm. The transverse curve in front carries on the angular curve of the back of the head, but it flattens out towards the rear, since the plate, which is almost straight in profile for rather than half its length, droops to the posterior angle.

The surface is covered with small, evenly spaced stellate tubercles similar to those on the other plates (Pl. 8, fig. 5), and there is no sign of the main lateral line, so conspicuous in coccosteomorphs but absent in pachyosteomorphs.

The chief feature of the concave visceral surface is the long median keel with its large intermuscular or carinal process at the rear (*ke*, Text-fig. 17). The keel varies in its forward extension, approaching closely to the anterior margin of the plate in one specimen (Pl. 8, fig. 2) but falling far short in a somewhat larger specimen (P. 50347). It keeps low with a sharp edge until it rises rapidly to form the process at about the middle of the length of the plate, and at the same time the edge splits to form the groove for grasping the neural spines of the vertebral column and continuing upwards behind to form an oval depression to grip the submediandorsal plate (Miles & Westoll 1968 : 423). The process is at the growth-centre of the plate some distance from the tip of the posterior spine, and there are the usual butresses, faint at the sides, far more marked behind where the process is produced backward, especially in the largest specimens (P.50357). There are no 'anteriorly facing pits', as mentioned by Miles & Westoll.

The areas overlapping the dorso-lateral plates are very well shewn. That for the anterior plate is unusually short and broad, that for the posterior plate exceptionally straight and narrow. The anterior area corresponds exactly with the smooth overlapped area on the anterior dorsolateral plate figured in Plate 7, and thereby fixes the limit of its missing hinder margin. The long narrow overlapping area of the median dorsal plate and the posterior margin of the anterior dorso-lateral plate mark the upper and anterior margins of the exposed surface of the missing posterior dorso-lateral plate, while the hinder ventral overlapped area of the anterior dorso-lateral establishes the front margin of the unknown posterior lateral plate.

The anterior dorso-lateral plate is represented by a single example, fortunately the fine almost complete specimen associated with the paranuchal previously mentioned

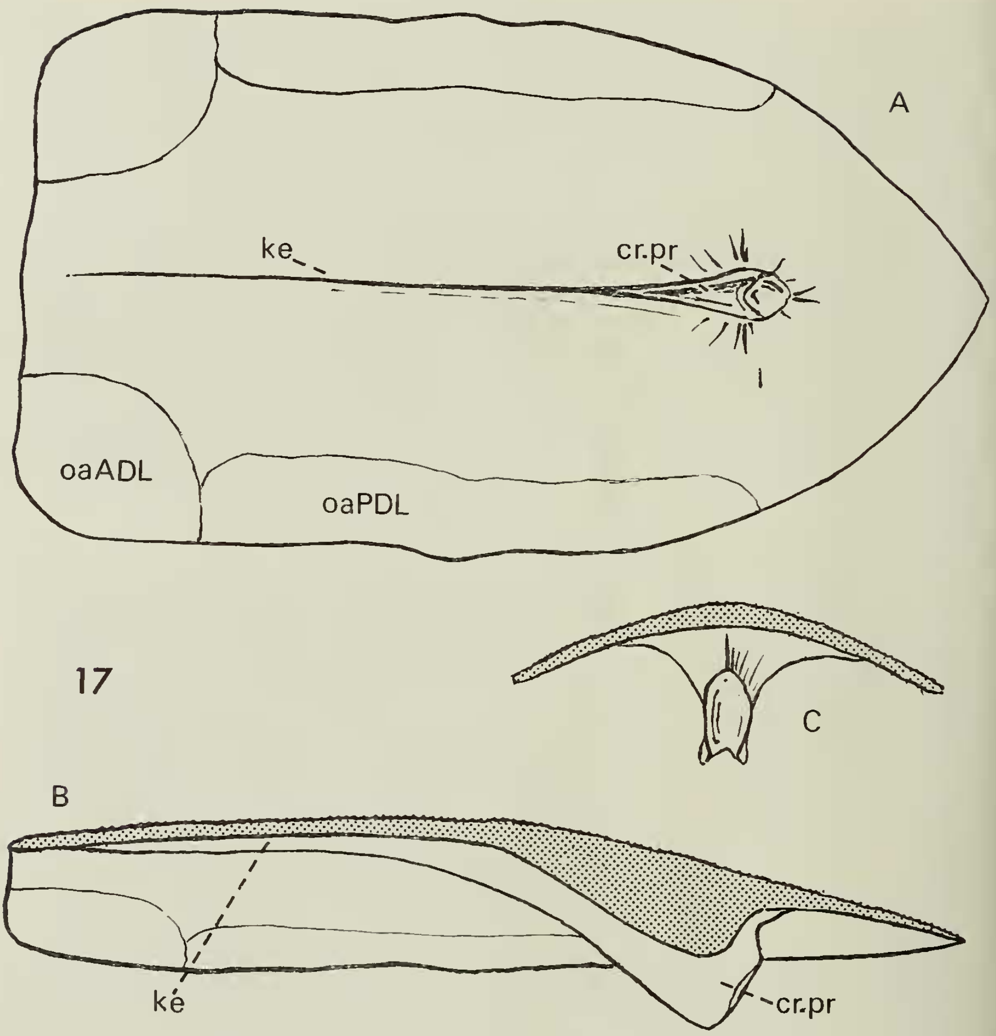


FIG. 17. *Parabuchanosteus murrumbidgeensis* (White).
Outline restoration of median dorsal plate. A, ventral view. B, left parasagittal view. C, posterior view of intermuscular crest. All ×1½. See Pl. 8, fig. 2.

(Pl. 7, figs 2, 4). Judging by the overlapping areas on the median dorsals there is only an oblique strip missing along the hinder border. The articular apparatus is very fully developed, both glenoid condyle and sub-glenoid process being very prominent, and as remarked above, they fit very closely into the process and fossa of the associated paranuchal plate.

The exposed area is relatively small, the plate being very short and the overlaps large, that for the median dorsal being almost square with a selvage for the extrascapular. The area overlapped by the anterior lateral is short, pointed, very wide and deeply grooved parallel with the front margin, and behind it, separated by an acute projection of the exposed surface and a ridge, is an overlapped area for the posterior lateral plate, which is, so far as we know, unique. The exposed surface of the plate is finely tuberculated, as on the other plates, and bears deeply incised grooves for the sensory lines, the plan of which fits in reasonably well with that put forward by Ørvig (1969*a*), their disposition (P.l 7, fig. 2) being similar to that on the same plate in *Holonema* (Miles 1971: 158, 191, text-figs. 68, 70). According to their interpretation the main lateral line, after a brief entry in a deep groove from the paranuchal plate gives off a short mesially directed 'accessory twig' (*lac*) and then

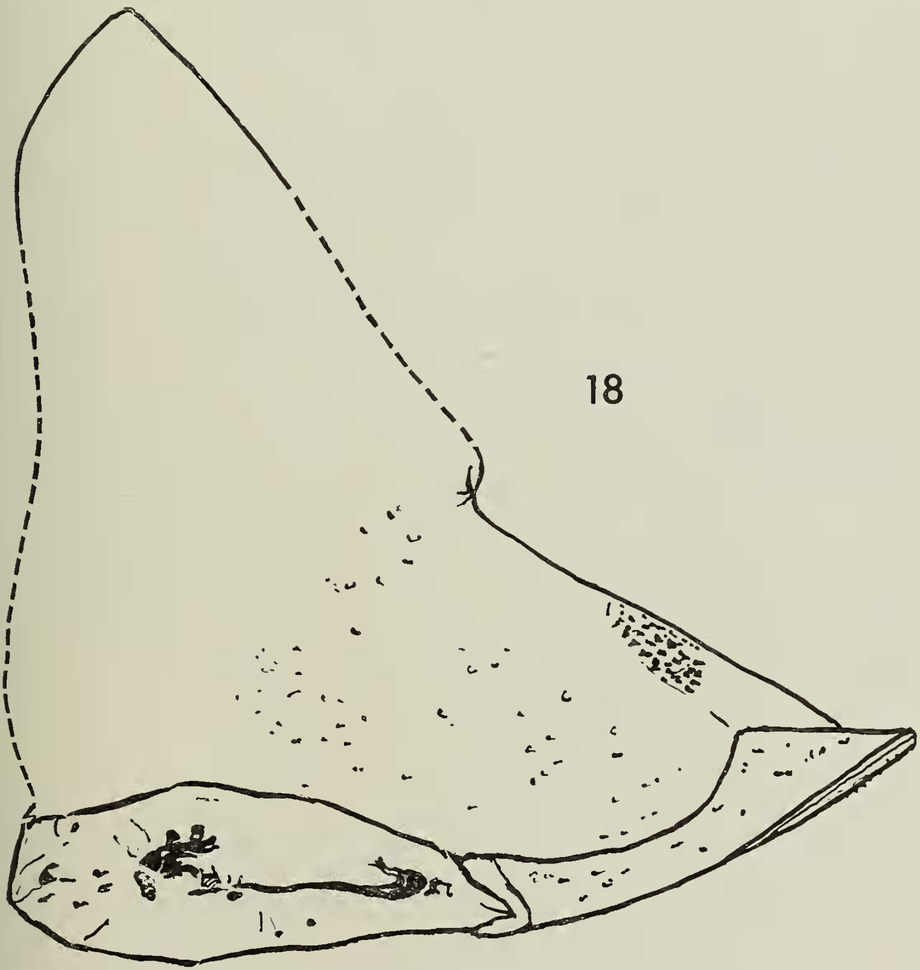


FIG. 18. *Parabuchanosteus murrumbidgeensis* (White).
Outline restoration of right anterior lateral plate based partly on overlapped area in anterior dorsolateral plate and partly on specimen P.50248 (Pl. 8, fig. 4), with socket of pectoral fin, and spinal plate. ×2 approx.

is interrupted, running after a short break in a narrower groove (*mlc*) more or less directly backwards, possibly on to the posterior dorsolateral plate (Text-fig. 24), while the deeper groove thereafter continues parallel, apart from a kink, to the sloping anterior lateral margin, presumably on to the posterior lateral plate and supposedly holding the ventrolateral sensory line (*lcvl*).

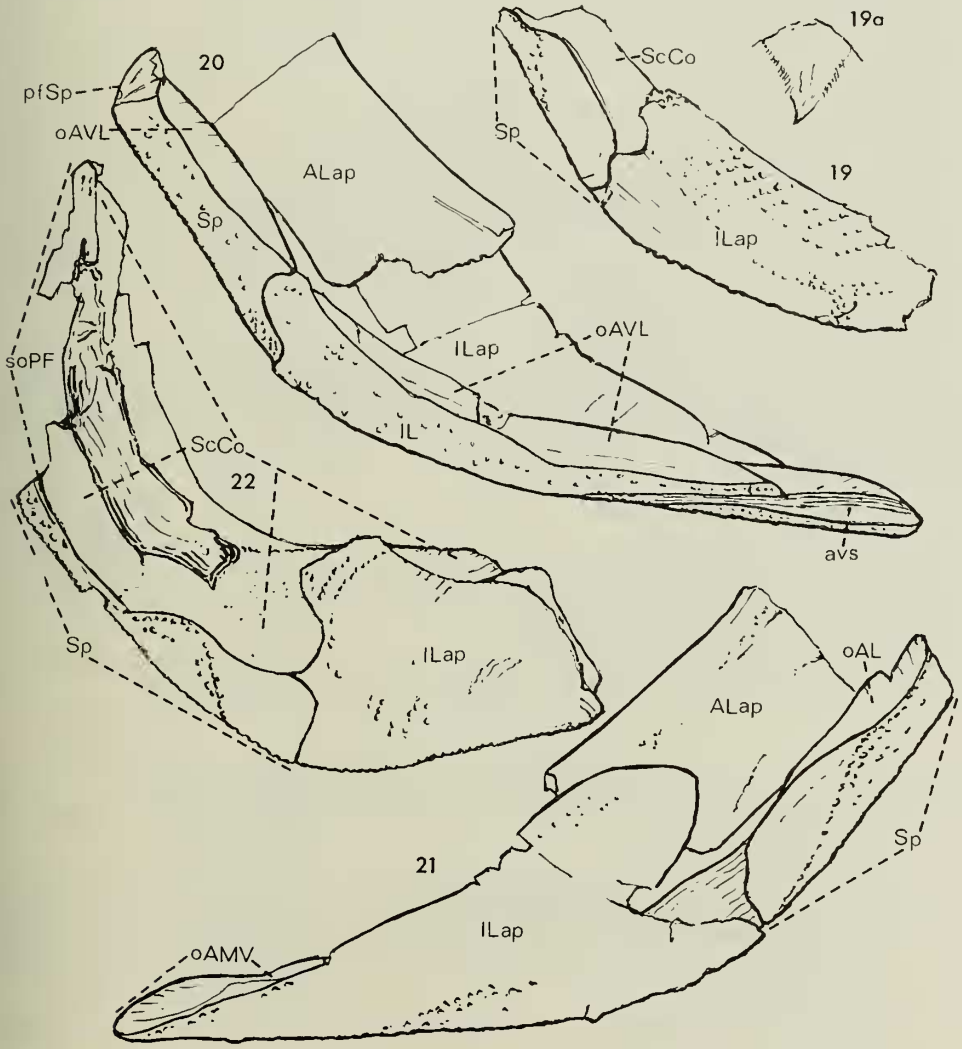
There is no indication of an anterior dorsolateral sensory line.

Of the missing posterior dorso-lateral plate we know only the length and curve of the upper margin from the underlaps on the median dorsal, but presumably it does not differ very much from the coccostean pattern (Miles & Westoll 1968, text-fig. 43).

With regard to the lateral plates there is equal difficulty. From the shape of the overlap on the anterior dorsal lateral plate, the upper end of the anterior plate was unusual, narrow and pointed, and the rather small specimen of the lower half assigned to this species is imperfect (Text-fig. 18; Pl. 8, fig. 4). The apron fits accurately on to that of the interlateral plate by which it is overlapped and the lower margin fits well on to the overlapped margins of the spinal plates. How far over the articular area of the scapulo-coracoid it extends it is not possible to be sure, but since the shoulder-girdle is distinctly coccosteomorph in character it is probable that it reached right over it to meet the posterior ventro-lateral plate. This basal part of the anterior lateral is very convex and sweeps round to the very broad upper part of the apron in an almost continuous curve for 90°. This part of the apron is, however, flattened and is roundly indented below by the overlap of the interlateral part and finishes at the upper end in a rounded point at the level where the side of the plate thickens and projects forwards, forming in this broken specimen a thick boss. The ornament on the sides is of the usual tubercular type, but this passes rapidly where it turns to form the apron into the special ornament of that part, which is best seen on a fragment of the interlateral plate (Text-fig. 19; Pl. 9, fig. 3). This ornament is similar to that in *Williamsapsis* (White 1952 : 265, pl. 28, fig. 1) but differs in detail and is somewhat variable: the teeth are less flattened, more finely striated and pointed and more strongly denticulated laterally: the ornament may be described as being composed of small depressed, biconvex, triangular teeth arranged in alternating rows and directed outwards with the upper surfaces finely striated with sharp downwardly curved points and finely but clearly denticulated along the sides except at the tips (Text-fig. 19; Pl. 9, figs 2–4). At the top outer part of the apron is a smooth area which is continued on to the spinal plate, a development apparently peculiar to this species.

Much of the apron with its special ornamentation is carried by the very long interlateral plate (Text-figs 19–22; Pl. 9) which, as suggested by Denison (1958 : 532), is true of *Williamsaspis*; the apron is very large and reaches from its spade-shaped overlap of the anterior lateral plate to the very tip in the centre. The interlateral (or clavicle) is very like that of *Coccosteus* (Miles & Westoll 1968 : 437, text-fig. 42) with anterior ventral sulcus (*avs*), groove for the coracoid process, and overlaps, but it is much longer with the details somewhat exaggerated, while the angle between the ascending and ventral laminae is much more acute. The ventral lamina is flat with the usual tubercular ornament and directed far more definitely upwards (Text-fig. 23).

The spinal plate (*Sp*, Text-figs 18–23; Pl. 9) is long and straight with no suggestion of a spine. The small triangular posterior face is almost flat with a shallow double groove to which perhaps the base of the fin membrane was attached. The slightly concave upper surface and the flat uptilted lower surface meet, like those of the interlateral, at a very acute angle, Stensiö's 'horizontal crest' (1959 : 8). The surfaces are uniformly ornamented with tubercles except that, as mentioned above, the upper anterior surface has a smooth triangular area in continuation of the



FIGS 19–22. *Parabuchanosteus murrumbidgeensis* (White). Sketches of specimens shewn in Pl. 9 with lettering. 19*a*, denticle of apron much enlarged.

apron of the interlateral plate. The interlateral overlaps the spinal both above and below, and there are also considerable areas overlapped by the anterolateral plate along the upper margin and by the anterior ventrolateral plate along the lower.

An interesting feature of the shoulder-girdle is the superficial ossification of the massive scapulo-coracoid (Text-figs. 18, 19, 22–24; Pl. 9, fig. 4), which is surprisingly strong. As Stensiö (1958 : 9) and Miles and Westoll (1968 : 443) have noted, an ossified coracoid process has not been found in the known coccosteomorphs, only in certain dolichothoracids, but presumably this is an effect of the general reduction in ossification and therefore an index of age and not of relationship. In section it is roughly triangular where it is broadest at the bend at the interlateral-spinal junction.

It is very broad indeed at this point and also deep (Text-figs. 22, 23), but narrows quickly towards the midline. Apparently it does not meet its antimere, for the groove in the interlateral stops some distance from the mesial tip where the latter turns upwards to overlap the anterior median ventral plate (*oAMV*, Text-fig. 21). Posterior to the spinal plate the scapulo-coracoid narrows gradually, becoming wedge-shaped behind the attachment area of the pectoral fin (*soPF*), which is very long, as long as the spinal plate, and here much of the articular surface remains, but the details of foramina are not well preserved.

Judging from actual specimens this part most nearly resembles, not unexpectedly, that of the spineless *Williamsaspis*, rather than that of *Pholidosteus* with its prominent pectoral spine (Stensiö 1959, text-figs. 9–11, 58), but it comes near enough to Stensiö's prediction for *Plourdosteus* (1959, text-fig. 12). Clearly this massive support must have borne a very large fin.

A fracture in the pre-coracoid part shews the inner surface with canals for dorsal cutaneous nerves and vessels.

A noteworthy character of this scapulo-coracoid is the smooth inner curve without any indication of scapular process (anterior mesial angle) or of post-pericardial angle. Presumably such simplicity is primitive.

Of the ventral plates of the body there is none that can be definitely associated with this animal that has sufficient margins to be worth description.

III. SUMMARY OF CHARACTERS

The outstanding features of *Parabuchanosteus murrumbidgeensis* are:—

1. Separate rostro-pineal bone and short wide preorbital plates with complete mesial contact.
2. Orbits large and directed obliquely forwards.
3. Sensory canal system and pattern of dermal head-bones as in brachythoracids with large broad-based nuchal more than one-half median length of shield.
4. Cervical articulation very well developed but skull apparently immovable on body armour.
5. Neurocranium wide and flat, fused to skull, not unlike that of *Kujdanowiaspis*.
6. Parasphenoid roughly triangular with strong but incomplete transverse groove and very small paired bucco-hypophysial openings.

23

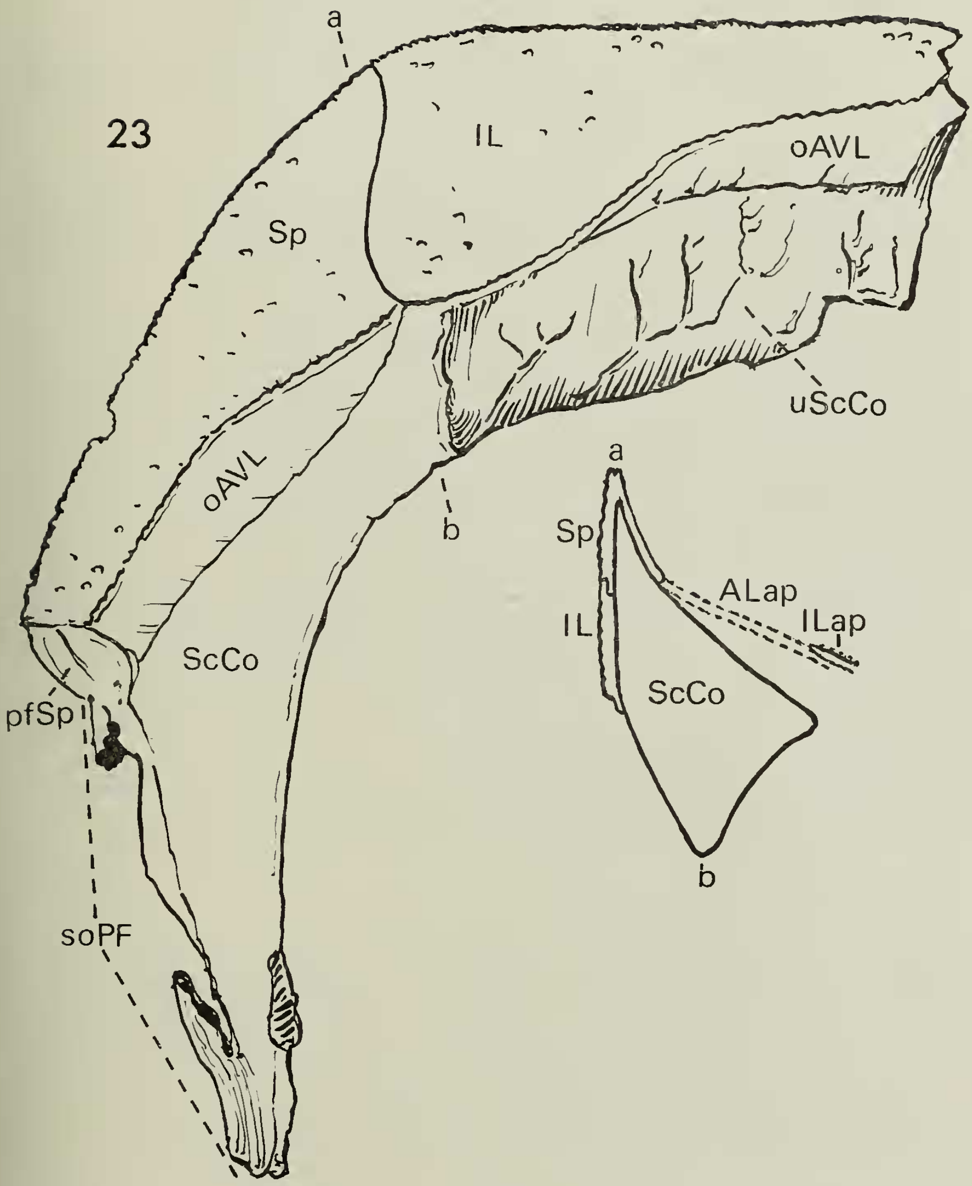


FIG. 23. *Parabuchanosteus murrumbidgeensis* (White). Sketch of underside of interlateral and spinal plates with scapulo-coracoid. Cross-section at *a-b*. Same specimen as in Text-fig. 22, ×2½.

7. Inferior division of fossa hypophyseos in stout capsular dorsal extension of parasphenoid.
8. Wide sub-pituitary fenestra below large pituitary sinus.
9. Neurocranial cavity with large anterior fenestra.
10. Posterior postorbital process tubular, carrying 1st branchial trunk of vagus.
11. Posterior face of endocranium with paired epiotic prominences separated by small supraoccipital spine.
12. Suborbital plate with strong suborbital bar and wide dorsal groove for articulation with skull-roof.
13. Infraorbital sensory canal prominent on suborbital plate, but supraoral canal does not meet it. Cheek-line (postsuborbital line) and pit for cutaneous sensory organ present.
14. Palatoquadrate strongly attached to inner face of suborbital plate.
15. Submarginal plate resembling that in *Coccosteus*.
16. Median dorsal plate long and narrow with blunt posterior angle, well developed median keel and carinal process.
17. Small anterior dorsolateral plate overlapped by posterolateral as well as by anterolateral and median dorsal plates.
18. Posterior dorsolateral plate with long upper margin overlapped by median dorsal plate.
19. Anterolateral plate with narrow pointed top and wider base and apron.
20. Spinal plate without spine, upper and lower surface almost flat meeting at very acute angle, and posterior face very small, triangular. Smooth area on front upper surface continued from interlateral, forming part of apron.
21. Interlateral long and tapering with wide apron behind, and upper and lower surfaces meeting at acute angle.
22. Scapulo-coracoid massive with relatively strong investment of perichondral bone; section curved triangular in coracoid region.
23. Base of pectoral fin long and fenestra equal to spinal plate in length.

The essentially dolichothoracid characters are in (1) and come reasonably close to Denison's diagram of *Kujdanowiaspis* (1958, fig. 105*F*).

The neurocranium (5) at first sight, like the palatoquadrate attachment (14) seem clearly dolichothoracid features and bear no resemblance to the corresponding parts in the two coccosteomorphs, *Pholidosteus* and *Tapinosteus*, in which they have been described. But as Stensiö (1959 : 55) has sagely observed, the differences may be 'due to the fact that *Pholidosteus* and *Tapinosteus* both are upper Devonian forms whose endocrania have, perhaps, undergone considerable modifications and reductions and therefore differ from the endocranium in the geologically older Coccosteomorphi, for example *Coccosteus*. Since, however, the endocranium is practically unknown in the latter Coccosteomorphs, the question concerning the mutual kinship between the Coccosteomorphi and Dolichothoraci must be left unanswered for the present.' It is possible that the answer does lie in *Parabuchanosteus* and that some at least of features 6–11 belong to the original common design.

Paragraphs 12, 15, 16, the general form of the known body-plates and the large orbit are undoubtedly coccosteomorph in pattern, but shew peculiarities of their own, and this applies to the spineless spinal plate, which although it does occur in the aberrant contemporary *Williamsaspis* is not, as we know them, typical of the dolichothoracids.

IV. RELATIONSHIPS

The information about *Parabuchanosteus* introduces some new factors in the vexed dispute about the relationships of two major groups of arthrodires, the brachythoracids and the dolichothoracids (arctolepids) which is briefly summarized by Denison (1958 : 536, 547), 'if one follows Stensiö in considering a wide-based pectoral fin to be primitive among arthrodires the Arctolepida could not have been ancestral to the brachythoraci'. The idea that the arctolepids were ancestral to the brachythoracids is the holy writ of virtually all other workers on the arthrodires, and their views at times have been expressed, we think, with rather more vehemence than the evidence warrants. To quote Denison further 'But with the exception of this purely theoretical consideration, there seems to be every reason for believing that the Brachythoraci were derived from the Arctolepida. In the first place, Arctolepida lived at the right time. Secondly, there are several forms known that are intermediate in structure . . .'. Which considerations are purely theoretical in this discussion and which are not is largely a matter of subjective interpretation and Stensiö's contention is no more theoretical than are many of his opponents' notions: it certainly has more reasons for acceptance than the sweeping statement that 'there seems to be every reason for believing that Brachythoraci were derived from the Arctolepida' which, taken literally, is just not true; and ten such trivial and largely quantitative characters as 'the supraorbital lines may extend . . .', 'the trunk shield is rather high . . .' and so on, are hardly worth serious consideration in this context. Furthermore, isolated adult forms, however well they may show intermediate characters, need prove nothing more than some degree of common ancestry without the evidence that one group was fully developed before the other: otherwise the evidence is equivocal and may be read either way (*cf.* Van Valen 1963 : 261).

The time of the first appearances of the two groups is the crux of the argument and Denison put as first of his 'every reasons' for the derivation of the bracyhthoracids from the arctolepids that 'Arctolepida lived at the right time'. But living at the right time is not quite the same as first appearance and it does seem that people have been influenced by maximum developments, which, however impressive, are totally irrelevant to the argument; but they are easily demonstrated and generally based on reliable evidence accumulated over the years, whereas first appearances are liable to be moved backwards by fresh discoveries and one more authenticated specimen can destroy the current argument.

Until the 'intermediate' forms, all from the Siegenian, had been properly evaluated the prior claim of the arctolepids seemed clear enough: according to Westoll (1967 : 84) the earliest arctolepids recorded appear to be indeterminable remains from the Clee district, while the heyday of the group was in the late Lower Devonian (Denison

1958 : 502–3); whereas the typical brachythoracids started with *Coccosteus* in the late Middle Devonian and (with the 'pachyosteomorphs') had their maximum development in the early Upper Devonian (Miles 1969 : 133). The supposedly wide gap between the first record of an arctolepid (?Upper Gedinnian) and the début of the brachythoracids (Givetian) seemed to provide logical, almost incontrovertible, evidence for the ancestral position of the former group, hence the 'cri du coeur' from Westoll (1958 : 203) that Stensiö had turned the geological succession upside down! The position has been considerably changed within recent years: the three so-called 'mixed' genera from the Northern Hemisphere, *Euleptaspis* (*Leptaspis* Gross, 1933 : 62; Ørvig 1960 : 305 footnote), the giant *Tityosteus* (Gross 1962) and *Gemuendenaspis* (Miles 1962), have all been accepted as true brachythoracids and all are from the Siegenian (Miles 1969 : 153).

On the other hand, of the five indeterminable fragments from the Welsh Borders, noted by Westoll (1967 : 84) as being of lowest Dittonian age and therefore probably representing the first dolichothoracid record, all but one rather insignificant and doubtful spine are actually higher in the succession than the specimens of *Heightingtonaspis* [*Kujdanowiaspis*] *anglica* (White 1961 : 26; 1969 : 305), of which the lowest comes from beds 600 feet above the 'Psammosteus' limestone and may be of early Siegenian age. So the difference between the earliest records of the two groups has been so reduced as to call into question the validity of the stratigraphical evidence in the argument.

Miles (1969 : 128, 147, 165) in his paper on placoderm diversification suggests that this took place rapidly after the appearances *inter alia* of heavy armour forming a separate head- and trunk-shield and a cervical joint, not long before they appear in the geological record, when the major taxa become distinct. The brachythoracids were derived, he suggests, from dolichothoracids, from unknown unspecialized ancestors at the base of the phlyctaenaspid stock, presumably without the specialization of the exaggerated pectoral spines of the familiar forms and possibly also of the considerable length of the body-armour. This would be in accord with the 'generally accepted view' which De Beer (1951 : 98) quotes 'that it is not possible to derive one form in phylogeny from another if the latter is too specialized'. Whether the length of the body-armour is a specialization is open to question. One of us has suggested (White 1952 : 296) that long body-armour of the dolichothoracids together with the long-based fin of the brachythoracids were characters of the common ancestor of the two groups, and this combination has persisted in the Siegenian brachythoracid *Gemuendenaspis* (Miles 1962) in spite of Denison's (1958 : 539) difficulty in imagining 'how this could be'. We still lean towards the common ancestor as being the true explanation of the origin of these groups and would suggest modifying Miles' idea so as to place the derivation of the brachythoracids at the base of the *actinolepid* stock.

At this point the pre-actinolepid might be indistinguishable from a common ancestor.

The case of *Parabuchanosteus* is very different from that of the Siegenian genera of the Northern Hemisphere mentioned above. Although its brachythoracid features are perhaps the more obvious, its dolichothoracid qualities are clear enough. It has,

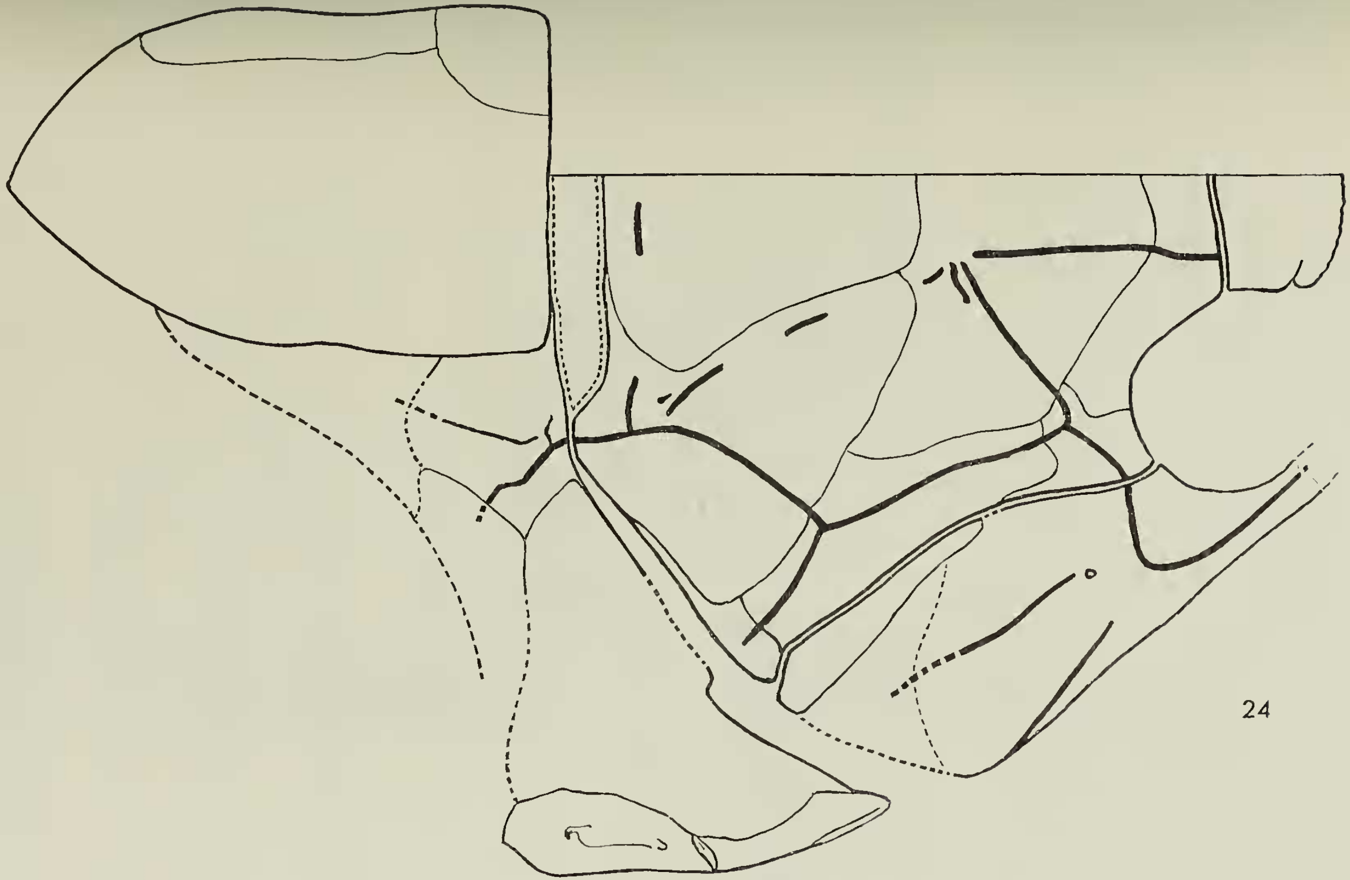


FIG. 24. *Parabuchanosteus murrumbidgeensis* (White).
Outline restoration of right side of head- and body-armour (median dorsal plate complete to shew overlaps).

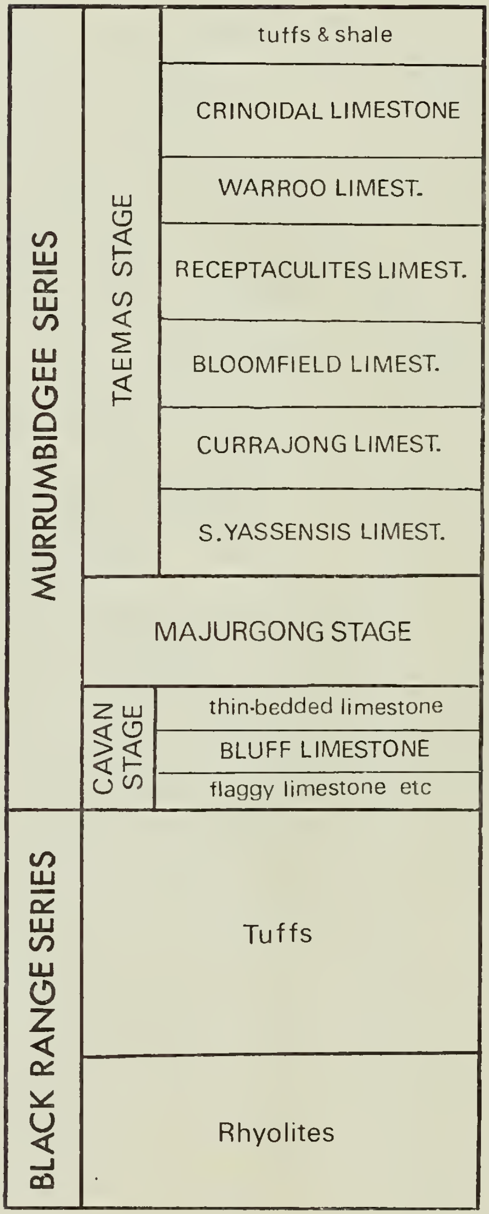


FIG. 25. The stratal subdivisions of the Taemas area. From Pedder, Jackson and Philip, 1970, after I. A. Browne, 1959.

of course, been acclaimed as a true intermediate between a dolichothoracid ancestor and a brachythoracid descendant, or, to put it another way, as a brachythoracid throwing off the last effects of a dolichothoracid past. But the distribution of the characters is odd—there is not so much of a mosaic effect about them as that of a linear series: dolichothoracid at the snout, normal brachythoracid over most of the skull-roof, and specialized brachythoracid (with perhaps even a touch of pachyosteomorph) body-armour. To claim that one part was more ancestral in type than the rest would conjure up a curious picture of a creature that was part of a phylogenetic assembly-line gradually moving up the scale, with a reactionary snout soon to be discarded and a progressive backside leading the way to better things. On the contrary we see *Parabuchanosteus* as a prime example of experimentation (Schaeffer 1965; 1967 : 1–6) in which coming events have cast a longer shadow than usual.

V. ACKNOWLEDGEMENTS

We are most grateful to Dr. H. W. Ball, Keeper of the Dept. of Palaeontology for hospitality in the department and to the authorities of the Museum for a generous grant towards travelling expenses.

To Dr. R. S. Miles, in charge of the palaeozoic fishes, we owe a debt of gratitude not only for his ready cooperation and patient help at all stages, particularly with his advice and invaluable information based on superb material from Western Australia, but also for allowing us the opportunity to examine this material.

From Drs Colin Patterson, Graham Elliott and Humphrey Greenwood we also received most useful information.

The specimens were prepared in acid by Messrs. R. Croucher, P. Whybrow and C. I. Macadie, and the photographs for the plates were taken by Mr. Peter Green, of the Museum Photographic Service.

VI. LOCALITIES

Localities, as written on labels, from which identifiable remains of *Parabuchanosteus* were collected by H. A. Toombs.

A. April to May 1955

1955.

2. *S. yassensis* Limestone
Not *in situ*, left bank of Murrumbidgee, on shore at bottom of scree slope below 'Shearsby's Wallpaper', 1100 yds upstream from Old Taemas Bridge. (=63/3). P.33202, P.33582, P.33583.

4. *S. yassensis* Limestone (near base)
Sloping ground immediately north of 'Shearsby's Wallpaper', 1700 yds at 154° magnetic from Taemas homestead. P.33592.

6. *S. yassensis* Limestone (near base)
Loose blocks near 55/5, not *in situ*, but probably nearly so. (=63/16). P.33597.

12. *S. yassensis* Limestone
Left bank of Murrumbidgee, 80 paces downstream from mouth of Oakey Creek, low cliff c. 1300 yds upstream from Old Taemas Bridge. P.33610.

14. *S. yassensis* Limestone
Spur above left bank of Murrumbidgee, 2250 yds bearing 55° magnetic to centre of New Taemas Bridge. P.33612.

15. *S. yassensis* Limestone
Loose blocks on hillside around 55/14 (*c. in situ*). P.33613, P.33618.

19. Bloomfield Limestone (near base)
Gully in left bank of Murrumbidgee, 3650 yds at 344° magnetic from Majurgong T.S. P.33629.

23. *S. yassensis* Limestone
Loose blocks *c. in situ*, on west limb of anticline and south slope of valley, 850 yds at 71° magnetic from Majurgong T.S. P.33635.

26. *S. yassensis* Limestone (near base)
On north side of hill, 1150 yds at 67° magnetic from Majurgong T.S. P.33642, P.51644.

32 & 33.
Near Bloomfield-*Receptaculites* boundary
On west side of main road, *c.* 100 yds N. of junction with road to Cavan: scattered blocks along strike line 50 to 100 yds from road, 1400 yds SSE of centre of new Taemas Bridge. P.33672, P.33673, P.33678, P.33683, P.53260.

x. ?Cavan Bluff Limestone
N. side of Bloomfield Rd, 1⅝ miles NE of Old Taemas Bridge, and 10 miles SSW of Yass. P.33430 (Colld. D. J. Cameron).

B. March-July 1963

1963

3. *S. yassensis* Limestone
Left bank of Murrumbidgee, 1100 yds upstream from Old Taemas Bridge, at bottom of scree slope below 'Shearsby's Wallpaper' (=55/2). P.48672, P.48674, P.50345, P.50346, P.50347.

7. *S. yassensis* Limestone (near base)
Right bank of Murrumbidgee, on shore, *c.* ½ mile downstream from Fifeshire Creek. P. 50357.

11. *S. yassensis* Limestone
Right bank of Murrumbidgee, *c.* ½ mile downstream from Fifeshire Creek, on NE point of small inlet. P. 50364.

12. Warroo Limestone (near base)
Right bank of Murrumbidgee at N end of cliffs, on shore, 2200 yds at 15° magnetic from Majurgong T.S. P.50367.

13. *S. yassensis* Limestone
Right bank of Murrumbidgee on shore, S. side of creek 1½ miles W of S of Alum Creek road-bridge. P.50378.

14. *S. yassensis* Limestone
Right bank of Murrumbidgee on shore, N side of creek 1½ miles W of S of Alum Creek road-bridge. P.50382.

16. *S. yassensis* Limestone (near base)
Left bank of Murrumbidgee on shore east of mouth of Oakey Creek, 1250 yds upstream from Old Taemas Bridge. P. 50389.

24. *S. yassensis* Limestone (near top)
Shore at south end of "Goodradigbee Lake", immediately east of where track from Barber's and Wee Jasper ends. P.50408.

25. *S. yassensis* Limestone (platy limestone near middle)
Shore at south end of "Goodradigbee Lake', east of 63/24. P.50416.

41. *S. yassensis* Limestone
Right bank of Murrumbidgee at most westerly point, 1850 yds at 24° magnetic from Majurgong T.S. P.50443.

58. Warroo or *Receptaculites* Limestone (near junction)
Right bank of Murrumbidgee, 3150 yds at 70° magnetic from Majurgong T.S. P.50808.

60. *S. yassensis* Limestone (low)
Right bank of Murrumbidgee, boulders probably nearly *in situ*, on shore and up hillside, 2500 yds due E of Majurgong T.S. P.50219.

66. *S. yassensis* Limestone
Left bank of Murrumbidgee, boulders on shore and hillside above, 1300 yds at 29° magnetic from Majurgong T.S. P.48675, P.48676, P.50248, P.50249.

68. *S. yassensis* Limestone
On hillside 1100 yds at 35° magnetic from Majurgong T.S. P.50252.

70. *S. yassensis* Limestone
Left bank of Murrumbidgee, on shore, probably *c. in situ*, 1400 yds at 62 magnetic from Majurgong T.S. P.50262.

83. *S. yassensis* Limestone
Top of spur falling west to left bank of Murrumbidgee, 1800 yds at 347° magnetic from Majurgong T.S. P.50323.

88. Crinoidal (? or Warroo) Limestone
Left bank of Murrumbidgee, scattered blocks on hillside 3650 yds at 9° magnetic from Majurgong T.S. P.50335.

DISTRIBUTION OF SPECIMENS

Specimen	Locality	Specimen	Locality
P.33202	55/2 (g)	P.33635	55/23
P.33430	55/X (a) (h)	P.33642	55/26
P.33582	55/2	P.33672	55/32 (c)
P.33583	55/2	P.33673	55/33 (c)
P.33592	55/4	P.33678	55/33 (c)
P.33597	55/6	P.33683	55/33 (c)
P.33610	55/12	P.48672	63/3
P.33612	55/14	P.48674	63/3
P.33613	55/15	P.48675	63/66
P.33618	55/15	P.48676	63/66
P.33629	55/19 (b)	P.50219	63/60

Specimen		Locality	Specimen		Locality
P.50248	—	63/66	P.50367	—	63/12 (e)
P.50249	—	63/66	P.50378	—	63/13
P.50252	—	63/68	P.50382	—	63/14
P.50262	—	63/70	P.50389	—	63/16
P.50323	—	63/83	P.50408	—	63/24
P.50335	—	63/88 (f)	P.50416	—	63/25
P.50345	—	63/3	P.50443	—	63/41
P.50346	—	63/3	P.50508	—	63/58 (d)
P.50347	—	63/3	P.51644	—	55/26
P.50357	—	63/7	P.53260	—	55/33 (c)
P.50364	—	63/11			

All specimens are from the *S. yassensis* Limestone except:

(a). ? From Cavan Bluff Limestone.
(b). From Bloomfield Limestone.
(c). From Bloomfield-*Receptaculites* boundary.
(d). From *Receptaculites* or Warroo Limestones.
(e). From Warroo Limestone.
(f). From Warroo or Crinoidal Limestone.

* * * * * * *

(g). Collected and presented by Mr. A. J. Shearsby.
(h). Collected and presented by Mr. D. J. Cameron.

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EXPLANATION OF LETTERING IN FIGURES

ADL	anterior dorsolateral plate
ad.n.cav	anterior depression (division) of nasal cavities
afcv	anterior fenestra of neurocranial cavity
ahm	articular surface (unossified) for hyomandibula
AL	anterior lateral plate (dorsal cleithral plate)
ALap	apron of *AL*
am.eth.sh	anterior margin of ethmoid shield
a.on + v.on	canal for the orbito-nasal artery and vein
arAL	area on *PNu* and *PM* overridden by *ADL* and *AL* (Stensiö's 'Sub-obstantic area)
arEsc	areas on both *PNu* + *Nu* and *ADL* overridden by extrascapular plate
arSO	area overridden by SO chiefly on *PtO*
aup	seating of autopalatine part of palatoquadrate on inner face of *SO*
AVL	anterior ventrolateral plate
avs	anterior ventral sulcus
b.V2	foramen or arch for the passage forwards of the lateral buccal and maxillary nerves
C	central plate
Cp.hyp.v	capsule of *fo.hyp.v* (extension of parasphenoid)
csc	central sensory canal
c.tel	cavity for telencephalon (and olfactory lobes)
c.v	cranial cavity
cr.pr	intermuscular or carinal process of *MD*
d.end	external aperture of endolymphatic duct
d.end.i	internal aperture of endolymphatic duct
dg	dorsal groove for vessels to *iws*
dls	dorso-lateral space for vessels to *iws*
dpmcu	cucullaris depression
dt	dermal tubercles inside nasal cavity
ehy	groove for efferent hyoid artery
Epio	epiotic prominence
eth.sh	ethmoidal shield (imperfect in fig. 8)
fbha	anterior, bilobate buccohypophysial foramina
fbhp	? posterior buccohypophysial foramen
fe.hyp.	fenestra hypophyseos in ventral endocranial wall
flv	levator pit for insertion of levator muscle of head
f.m	foramen magnum
fno	canals of subdivided olfactory nerve (I)
f.nv	orbito-ethmoidal foramen or slit (*sl.oe*, Stensiö 9163 : 206, fig. 72*B*, etc.)
fo.hyp.v	inferior division of fossa hypophyseos situated between *Psph* and endocranium
fsp	sub-pituitary fenestra
gc	glenoid condyle (articular trochlea of post-temporal plate of Stensiö 1963, etc.)
gda	groove for dorsal aorta
gf	glenoid fossa (lateral articular fossa of Stensiö 1963, etc.)
gp	glenoid process (occipital para-articular process of Stensiö 1963, etc.)
gra	groove for 'Rachendachhypophyse'
gr II	groove for optic nerve
hc	anterior part of supramaxillary (supra-oral) sensory line
hc 2	cheek-line (post-suborbital line)
ic	possible position of internal carotid artery
ifp	infranuchal pit
IL	interlateral plate (clavicle)
ILap	apron of IL

inr	median infranuchal ridge
ioc	infraorbital sensory canal
iw	internasal wall
iws	internasal wall-space
IXph	canal for pharyngeal branch of IX
ke	median keel under MD
lac	'accessory twig' sensory line
lcvl	ventrolateral sensory line
ld	dorsal branch of main lateral line canal
lv	lateral hypophysial vein
M	marginal plate
m.cd	dorsal attachment scars of m. constrictor dorsalis
m.chy	dorsal attachment scars of m. constrictor hyoides and possibly also for m. adductor mandibulae
mlc	main lateral line canal
mp	middle pit-line groove
MD	median dorsal plate
nda	naturally decayed areas
nmv	naso-maxillary vein
noe	position of exhalent nostril
noi	position of inhalent nostril
Nu	nuchal plate
oaADL	area under *MD* overlapping *ADL*
oAL	area overlapped by *AL*
oAMV	area of *IL* overlapping anterior median ventral plate
oAVL	area of *IL* and *Sp* overlapped by *AVL*
oaPDL	area under *MD* overlapping *PDL*
occ	occipital cross-commissural sensory line
oMD	area overlapped by *MD*
oNu	area overlapped by *Nu*
oph.l	lateral ophthalmic nerve canal
oph.V	superficial ophthalmic nerve canal
oPL	area overlapped by *PL*
orb	orbit
pcv	posterior cerebral veins
pi	probable position of pineal opening
pd.n.cav	posterior depression of nasal cavity
pfSp	posterior face of *Sp*
plae	posterolateral angle of endocranium (=supravagal process and craniospinal process in coccosteids)
p.lat.pr	posterior lateral process of subnasal shelf
PM	postmarginal plate
pmc	postmarginal sensory canal
pnw	posterior face of postnasal wall
PNu	paranuchal plate
pp	posterior pit-line groove
pq.m	seating of middle part of palatoquadrate on inner face of *SO*
PrO	preorbital plate
prpoa	anterior postorbital process
prpop	posterior postorbital process
pr.pvl	posteroventral palatine process
psba	canal of efferent pseudobranchial artery
Psph	parasphenoid
pt.my	posterior myodome

PtO	postorbital plate
pt.si	sinus of pituitary vein
p.V2,3	passage for maxillary and mandibular nerves
rcr	roof of cranial cavity at fenestra
rcv	roof of cranial cavity
r.la.c	remains of labyrinth cavity
RP	rostro-pineal plate
rpto	postorbital ridge
sb.sh	sub-orbital shelf
ScCo	scapulocoracoid
sgp	sub-glenoid process
shy	canal for hyoid vein
sns	sub-nasal shelf
SO	suborbital plate
SOa	articular head for *SO*
soc	supraorbital sensory canal
soPF	socket for pectoral fin (pectoral fenestra)
sos	supraoccipital spine
Sp	spinal plate
spio	canals of spino-occipital nerves
th.n	endolymphatic thickening
u.end	undersurface of endocranium
uScCo	inner surface of perichondral cover of coracoid process with canals for dorsal cutaneous nerves and vessels
V2,3	profundus canal
vca	anterior cerebral vein
vcr	vessels to cranial roof complex
vdm	canal for vein on posterior face of occipital region
VI	abducens canal
VIIhm	hyomandibular branch of facialis canal
vju	canal for jugular vein
vju.p	posterior aperture of canal for jugular vein
vmh	median hypophysial vein
v.on	orbito-nasal vein
vrm	veins draining roof of mouth
vse	ventral surface of endocranium
X	vagus canal
X_1	canal for first branchial trunk of vagus nerve
$X_?$	canal for second branch of vagus or the post-cerebral vein